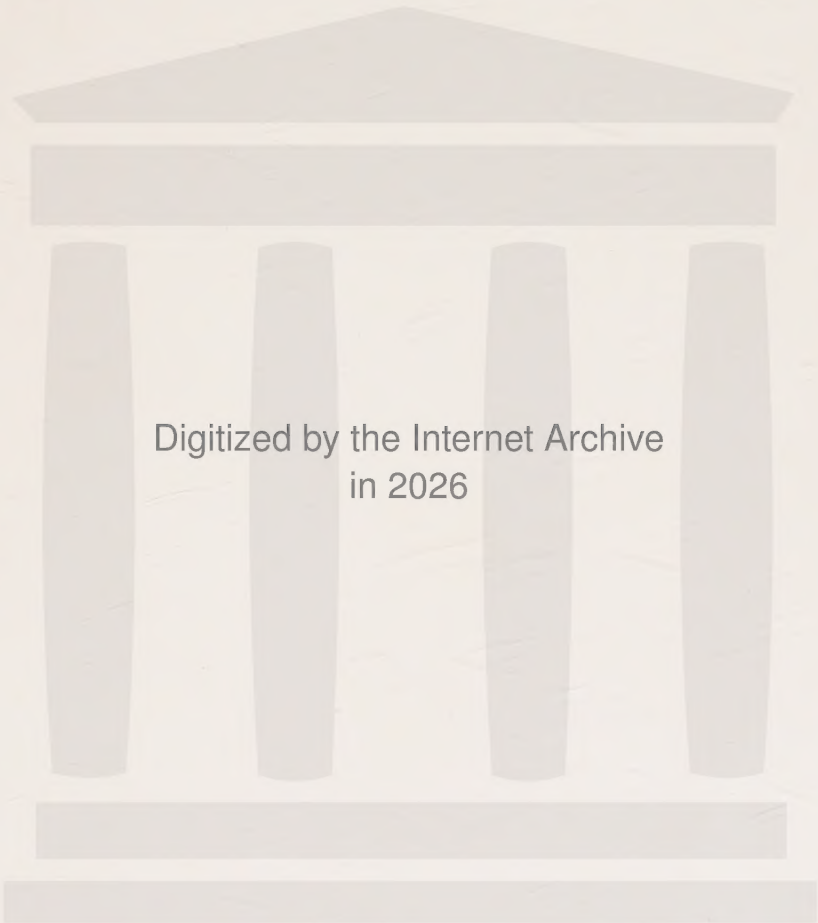
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A TEXT-BOOK

OF

GENERAL LICHENOLOGY,

WITH DESCRIPTIONS AND FIGURES OF THE GENERA
OCCURRING IN THE
NORTHEASTERN UNITED STATES.

BY

ALBERT SCHNEIDER, M. S., M. D.,

Fellow in Botany, Columbia University, 1894–1896.

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PREFACE.

This work is primarily intended as a text-book for the use of students in colleges and universities, but will also be found useful to the specialist. Although the title designates it as a text-book of *general* lichenology, the discussion of the Basidiolichenes and more or less problematical Gasterolichenes has been omitted, since these orders are not represented in the northeastern United States.

The systematic arrangement of the families and genera here proposed is by no means perfect, yet it is hoped that some progress has been made toward establishing a natural system. The fact that most arrangements heretofore proposed had little scientific basis is due to the lack of knowledge of the morphology and physiology of these plants. Even now our methods of physiological investigation are too imperfect to allow us to obtain any satisfactory data in regard to the life-history of the individual lichen. Until our methods of investigation are more perfect, all systems of classification must of necessity be more or less artificial and subject to changes.

In lichenology the conception of genus and species is vague and uncertain. This is the chief reason why every lichenographer has introduced or sought to introduce a new system, and as a result we have about as many systems as there are authors. Within comparatively recent years various investigators have studied lichens from a scientific point of view, especially from the standpoint of morphology. Of these morphologists may be mentioned Hedlund, Lindau, Minks, Reinke, Schwendener, Zahlbruckner and Zukal. Among those who have studied lichens from a physiological standpoint Bonnier and Jumelle deserve special mention. The arrangement of families and genera here adopted is based upon morphological data and is in accordance with the results of recent investigations.

In agreement with Reinke, lichens are treated as a distinct class, coequal in systematic importance with the fungi and algae. The present conception of the class Lichenes is, however, essentially differ-

ent from that of the older authors, such as Tuckerman and others, being in a great measure the outcome of recent investigations in symbiosis. For this reason it was thought advisable to include a chapter on the more common phenomena of symbiosis, which, it is hoped, will enable the student to obtain a better knowledge of the true nature of lichens.

Part II. treats of the special morphology of the families and genera of lichens occurring in the northeastern United States. The drawings (with the exception of Plate 5) were made by Mr. F. Emil, under the author's supervision. Duly considering the difficulties usually encountered in making drawings of this kind it is believed that they give a fairly accurate presentation of the histological characters of the genera occurring in the territory.

It is hoped that this work will act as an incentive toward leading others to the more scientific methods of studying this interesting group of plants. With Reinke, I wish to emphasize the necessity for studying more carefully the polyphyletic origin and relationship of the various lichen groups. This will, no doubt, lead to a more accurate delimitation of the families, and incidentally also to a more accurate knowledge of the phylogeny of other plants.

Columbia University, May 31, 1897.

GLOSSARY.

Antagonistic symbiosis, a form of symbiosis in which one of the symbionts is benefited at the expense of the other; usually known as parasitism.

Apothecium (**Apothecia**), the spore-bearing structure of lichens, including epithecium, thecium, hypothecium and exciple.

Areolate, a term referring to a crustaceous thallus which is marked off into minute, usually polygonal areas.

Breathing pores, intercellular canals in the cortical layers leading from the interior of the thallus to the exterior.

Cephalodium (**Cephalodia**), usually a globular, flattened or irregular outgrowth from the upper or lower surface of the thallus, induced by foreign algae and bearing them.

Contingent symbiosis, a form of symbiosis which is not constant in its occurrence. (Incipient symbiosis. Raumparasitismus.)

Cortex, see **Cortical.**

Cortical layers, pseudo-parenchymatous tissue (upper and lower) of the thallus of the higher lichens.

Crustaceous thallus, a firmly adherent thallus of lichens devoid of distinctly cortical layers.

Cuticle, see **Epidermis.**

Cyphella (**Cyphellae**), a pit or depression in the under surface of the thallus of most Stictei (*Sticta* and *Stictina*). They are neoformations analogous to lenticels.

Endospore, the inner coat of the spore-wall.

Epidermis, the thin horizontal scaly layer on the upper surface of the higher foliose lichens.

Epilithic, a term applied to the parts of lichens occurring on and above the surfaces of rocks.

Epiphloeodal, occurring on the surface of the bark.

Epispore, see **Exospore.**

Epithecium, the upper colored structureless coating of the thecium.

Exciple or **Excipulum,** the outer covering of the apothecium; when formed by the thallus and bearing algae it is known as thalloid exciple; when formed by the perithecium and not bearing algae it is known as proper exciple.

Exospore, the outer coat of the spore-wall.

Fibril or **Cilium,** a slender filament, consisting of united hyphae, usually occurring on the margin of the thallus.

Foliose thallus, an expanded entire or lobed thallus, having one or two cortical layers, usually attached by rhizoids. Also known as foliaceous or frondose thallus.

Fruticose thallus, a thallus consisting of rounded or flattened, vertical or ascending branches. Also called fruticulose thallus.

Gonidium (**Gonidia**), a term applied to the symbiotic algae of lichens.

Granule (adj. **Granulose**), a minute thalloid elevation firmly adherent to the substratum, usually bearing an indistinct upper cortical layer.

Hymenium, see **Thecium**.

Hypolithic, occurring below the surfaces of rocks.

Hypophloeodal, referring to that portion of the thallus or other structure of lichens occurring beneath the surface of the bark.

Hypothecium, the dense hypal tissue immediately below the thecium.

Individualism, a form of symbiotic relationship existing between two or more organisms in which the resulting organic structure is wholly different from any of the symbionts and in which at least one of the symbionts cannot exist independently.

Isidium (**Isidia**), a small cylindric simple or branched thalloid outgrowth from the surface of the thallus.

Medulla, the loose hyphal network in the interior of the thallus.

Mutualism, a form of symbiosis in which the symbionts are mutually beneficial.

Mycorhiza, a term applied to the symbiotic association of fungi and roots of higher plants (especially *Cupuliferae*). Divided into endotrophic and ectotrophic mycorhiza according to whether the fungi occur within the parenchyma-cells of the root or upon their exterior.

Mycodomatiae, term applied to the group of symbiotic organisms (*rhizobia*) which have the power of inducing tubercular neo-formations in the roots of plants.

Nutricism, a form of symbiosis in which only one of the symbionts is especially benefited.

Paraphysis (**Paraphyses**), a slender simple or more rarely branched, sterile filament among the spore-sacs.

Perithecium, the hyphal tissue of the so-called Pyrenolichenes (*Verrucariaceae*) enclosing the thecium.

Phyllocladium (**Phyllocladia**), a small highly assimilative branch of fruticose thalli. (This term is often applied to all secondary thalli.)

Podetium (**Podetia**), the elongated alga-bearing apothecial stalk of lichens developed from the primary thallus. (Usually applied to the vertical thallus of a *Cladonia*.)

Primary thallus, a term referring to the thallus from which the podetia develop.

Pycnidium (**Pycnidia**), the structure upon the thallus of lichens containing the so-called stylospores. (Perhaps closely related to the spermagonium.)

Rhizoids, special hyphal elongations from the under surface of the thallus which enter the substratum.

Secondary thalli, thalloid outgrowths from the thallus and podetia of lichens. Sometimes also applied to the podetia of *Cladonia.*

Seta (Setae), see **Fibril.**

Soredium (Soredia), a minute spherical body consisting of algae enclosed by a hyphal network and having the power of developing into a new lichen.

Spermagonium (Spermagonia), the structure upon the thallus containing the so-called sterigmata and spermatia.

Spermatium (Spermatia), a spore-like body formed in the spermagonium. (Considered by Stahl and others as the male reproductive organ of lichens.)

Spore-sac, the closed sac-like structure in which the spores are formed.

Squamule, a small entire thalloid lobe. Usually forming the transition to the typical foliose thallus.

Sterigmata, the filaments of the spermagonium bearing the spermatia.

Stipe, an apothecial stalk free from algae *(Caliciaceae* and *Baeomyces).*

Symbiosis, a contiguous association of two or more organisms accompanied by an interchange of assimilated food-substances.

Thallus (Thalli), the vegetative and assimulative portion of lichens, bearing the apothecia and soredia.

Theca (Thecae), see **Spore-sac.**

Thecium (Thecia), the layer consisting of thecae and paraphyses.

Umbilicus, the single root-like attachment of certain lichen-thalli *(Umbilicaria, Gyrophora).*

Verrucose, see **Warty.**

Warty, referring to a thallus bearing numerous thalloid elevations larger than the granules.

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PART I.

THE HISTORY, GENERAL MORPHOLOGY AND PHYSIOLOGY OF LICHENS.

CHAPTER I.

THE HISTORY OF LICHENOLOGY.

INTRODUCTION.

The lichens were more generally neglected by the early botanists than any other group of plants. The causes for this are not far to seek. These plants possess no qualities to make them conspicuous; they are not, as a rule, striking in color, size or form, nor do they possess very marked useful or harmful properties. Until the advent of scientific botany, herbalists devoted their attention chiefly to the higher plants, which were endowed with real or imaginary medicinal properties, or which served some other use in the household.

Later, when lichens began to receive some attention from the leading botanical systematists, they were for a long time subject to great abuse because of careless study. They were taken up as a side study for the information of the few who took a momentary interest in them. Some of the most fantastic and varied opinions were held with regard to their origin, nature and position in the vegetable kingdom. For these reasons and others, which will become apparent later, it was thought not only interesting but highly important that the student of lichenology should have an insight into the changes which this special science has undergone. It is hoped that the student may better realize therefrom how much work must yet be accomplished before our knowledge in regard to these plants can attain any degree of perfection.

The historical review here presented is, in the main, a condensed retrospect of Krempelhuber's Geschichte der Lichenologie. The limitations of the first four periods correspond to those of Krempelhuber; the others are materially changed, and the review has been

completed to the beginning of 1897. Other works treating of the history of these plants, notably Lindsay's British Lichens have also been made use of.

Each period is marked by some special evolutionary progress in lichenology. It must not be supposed, however, that these periods are in reality clearly and distinctly separated. One period gradually merges into the other, which makes the distinction more or less accidental or arbitrary. There are no doubt minds that tower above their contemporaries and whose works are to a certain degree epoch-making; on closer examination it is found, however, that they have built upon the foundation laid by workers that have gone before.

Only a few of the more important investigators in lichenology are mentioned. It would be impracticable as well as unnecessary to refer to all the authors who have written on the subject. The publications issued number thousands; to collect and digest these would be the work of many years. The references cited as footnotes are primarily of historic interest. The more important references to works having real scientific value are given on pp. xi–xvii. In order to avoid repetition these are referred to by number, where they are mentioned in the historical review, or in the text proper.

It is thought most appropriate and convenient to divide the history of lichenology into seven periods, as follows:

I. Period: From Theophrastus (371–286 B. C.) to Tournefort (1694).

II. Period: From Tournefort (1694) to Micheli (1729).

III. Period: From Micheli (1729) to Weber (1779).

IV. Period: From Weber (1779) to Wallroth and Meyer (1825).

V. Period: From Wallroth and Meyer (1825) to Schwendener (1868).

VI. Period: From Schwendener (1868) to Reinke (1894).

VII. Period: Beginning with Reinke (1894).

I. PERIOD.

From Theophrastus (371–286 B. C.) to Tournefort (1694).

The earliest references to lichens are all more or less unreliable. There is little doubt that lichens were known, but they were looked upon as mosses, algae or fungi, and classified with these

under such comprehensive terms as muscus, bryum, sphagnum. The term lichen (λειχήν) was doubtless used to designate various liverworts, especially species of Marchantia. Only after a much later period was this term employed exclusively in application to lichens. Historians are uncertain as to what plant or plants Dioscorides and Plinius intended to designate by the term lichen; it was in all probability a species of Marchantia or other liverwort.

The first somewhat authentic references to lichens are to be found in the writings of Theophrastus,[1] a pupil and follower of Aristotle. It is generally conceded that this eminent naturalist described several plants which were doubtless lichens. The very imperfect descriptions are supposed to refer to *Usnea barbata* and *Rocella tinctoria*. No further record seems to have been made of lichens until the first century of our era when Dioscorides and Plinius again mention the lichens supposed to have been described by Theophrastus. There is little doubt that these authors referred to *Rocella tinctoria* as a "marine fungus growing upon rocks, possessing coloring properties." *Usnea* no doubt attracted attention because of its remarkable development.

During the dark ages few observations were made on lichens, in fact all scientific progress came to a standstill. Only plants of evident or imaginary medicinal or economic uses were studied. It is remarkable that a period of over seventeen centuries elapsed during which nothing was added to the knowledge of lichens. Ruellius,[2] Dorstenius[3] and Gesner,[4] the first commentators on the writings of Theophrastus, Dioscorides and Plinius did little more than to reiterate what had been known of the two lichens above mentioned. We may safely state that up to time of Fuchsius[5] scarcely anything was known of lichens. There can be little doubt that various lichens came to the notice of botanists and herbalists of the time, but they were not thought of sufficient importance for special study.

Then followed a number of botanists who incidentally observed and described a few lichens with which they came in contact during

[1] A Latin translation by J. Bodaeus. Theophrasti Eresii de Historia Plantarum Libri Decem. 156. Amstelodami. 1644.

[2] Ruellius, J. De Natura Stirpium Libri III. Paris. 1536.

[3] Dorstenius. Botanicon continens Herbarum aliorumque Simplicium quorum usus in Medicinis est, etc. Frankfurt. 1540.

[4] Gesner, K. Historia Plantarum. Basel. 1541.

[5] Fuchsius, L. De Stirpium Historia Commentarii. Basel. 1549.

their collecting trips. We shall mention only a few of these botanists, especially those who were active in the various provinces of Germany and Austria, as well as in other countries of continental Europe. They were Mathiolus,[1] Caesalpinus,[2] Camerarius,[3] C. Bauhin,[4] Clusius[5] and J. Bauhin.[6] These and various other authors discovered and described in all about twenty-eight kinds of lichens: mostly species belonging to the genera *Usnea*, *Sticta*, *Cetraria* and *Cladonia*. The descriptions and attempts at illustration were indeed very defective, so that later authors were often at a loss to know what species was really meant.

Up to this epoch lichens had been given no definite position in the vegetable kingdom. They were variously classified with algae, fungi, liverworts and mosses. About this time also we find the first record of observations made on the development and reproduction of Lichens. Porta[7] gave some very crude explanations of the origin and growth of Lichens. Malpighi[8] was the first author to demonstrate the presence of soredia. He also observed that these structures were propagative organs and for that reason considered them as true seeds. One of the most active lichenologists of this period was the Scotch botanist Morison.[9] He described fifty-six species in all, of which ten were new; he also gave fairly good illustrations of about twenty-one species. This observer paid little attention, however, to the development of these plants, as is evident from his belief that lichens were excrementitious matter produced by the earth, rocks and trees.

This brief retrospect gives some idea of how little was known of lichens at the close of this period. Only such forms as were remarkable for their size, color or use in medicine received any attention. The use of *Rocella tinctoria* in the processes of dyeing

[1] Mathiolus, P. A. Commentarii in libros VI Dioscorides de Materia Medica. Venice. 1565 and 1583.

[2] Caesalpinus, A. De Plantis Libri XVI. Florence. 1583.

[3] Camerarius, J. De Plantis Epitome Utilissima, P. A. Mathioli Senensis. Frankfort-on-the-Main. 1586.

[4] Bauhin, C. Phytopinax seu Enumeratio Plantarum Nostro Saeculo Descriptarum. Basel. 1596.

[5] Clusius, C. Historia Plantarum Rariorum cum Appendice et Auctoria et Figuris 1135. Antwerp. 1601.

[6] Bauhin, J. Historia Generalis Plantarum Novae et Absolutae Prodromus. 1619.

[7] Porta, J. B. Phytognomonica VIII Libris Contenta. Frankfort. 1591.

[8] Malpighi, M. Opera Omnia. London. 1686.

[9] Morison, R. Historia Plantarum Universalis Oxoniensis. 1680, 1699, 1715.

was doubtless known before the time of Pliny. It is generally supposed that the blue and purple of the Old Testament (Ezekiel, XXVII. 7) refers to the dye made from this lichen. It is certain that it had formed for a long period an important article of commerce.

After the fall of the Roman Empire the knowledge of the use of this dye seems to have been lost. In the year 1300, Federigo, a Florentine of German parentage, accidentally rediscovered the method of preparing and using it; he is said to have achieved such success in his commercial transactions with this substance that in time he became the head of a distinguished family, the Oricellarii, who were later known as Rucellarii and Rucellai. From these names are derived orseille, the name of the coloring substance, and *Rocella*, the genus of lichens from which orseille is prepared. For more than a century Italy supplied the market with orseille derived mainly from lichens collected on the islands of the Mediterranean. After the discovery of the Canary islands in 1402 much of the orseille was derived from those islands, and later from the Cape Verde islands. Later orseille was collected from other islands and countries. It was also found that other genera besides *Rocella* furnished excellent dyes; for example, *Lecanora*, *Pertusaria*, *Umbilicaria*.

Like other practically inert plants, lichens were supposed to have medicinal properties. *Sticta pulmonaria* was strongly recommended in diseases of the lungs. Dorstenius was the first to give a more exact description and illustration of this lichen. He also described the medicinal preparations made therefrom, and their special therapeutic properties. Because lichens were supposed to have a strong retaining power for various odors and scents they were much used in the preparation of certain perfumes. Some of the fruticose lichens were especially recommended for this purpose. They formed the basis of the renowned Cyprian hair powder (*Pulvis Cyprius*), which was supposed to remove dandruff and to promote the growth of hair. Because of the astringent and bitter principles in some species of lichens they were used in tanning and brewing. The beer of a certain Siberian monastery which was noted for its peculiar bitterness owed this to *Sticta pulmonaria*. Lichens also found a temporary use in the manufacture of paper, pasteboard and parchment.

The "miraculously" supplied manna of the Israelites in the wilderness is supposed to have been a species of Lecanora (*Lecanora*

esculenta). This lichen occurs very plentifully in Algeria and Tartary, as well as in mountainous districts of other countries. The plant seems to grow and spread rapidly and, being loosely attached, the wind readily carries it down the mountain-sides into the valleys, where the ignorant inhabitants suppose it to have "rained from heaven." Travelers in the above countries have reported several noteworthy and extensive "rains of manna." The Kirghiz Tartars eat this lichen, under the name of "earth-bread."

Various other lichens were also used as articles of diet; among them *Cetraria Islandica* takes perhaps first rank, as it contains a high percentage of lichen-starch (lichenin). However, from the fact that nearly all lichens contain a bitter principle which is very disagreeable to the taste, they were extensively eaten only in arid countries and in times of famine.

II. PERIOD.

From Tournefort (1694) to Micheli (1729).

As already stated, the lichens were given no definite position in the vegetable kingdom in the previous period. Under the collective name "muscus" or "musco-fungi" (Morison), they were variously classed as algae, fungi, liverworts and mosses. The fact which separates this period from the preceding is that lichens were now being looked upon as a distinct class of plants. Tournefort[1] was doubtless the first to separate these plants from others and to arrange them as a distinct class under the comprehensive designation "lichens." This in itself was indicative of considerable progress. A group of plants must be given some definite position in the vegetable world before it can receive more careful study. Tournefort was one of the few investigators of his time who believed in laying a foundation before beginning to build. He did not concern himself so much with species-making as with a general study of lichens. In all his works he does not describe more than forty-four species and varieties, although fifty-six species and varieties were already known. This noted botanist, who was by no means especially interested in lichens, devoted his limited attentions to them taken collectively, and this led him to arrange them as a separate class.

[1] Tournefort, J. P. de. Elements de Botanique. Paris. 1694. Institutiones Rei Herbariae. Paris. 1719.

His illustrations also lead us to believe that he had more or less correct conceptions of the spores and apothecia. It is much to be regretted that Tournefort did not explain his illustrations more fully; to make matters worse later commentators have variously misinterpreted his explanations. When we consider the imperfection of the magnifying lenses at that time we can not help admiring the excellent work done by this French savant.

Plukenet[1] and Petiver[2] described several new species. They also added some comparatively accurate illustrations. Vaillant[3] likewise added a number of good illustrations, besides describing several new species. New species were also described by Ray,[4] Morton[5] and others.

There were other botanists of various countries who described species of lichens already known and added here and there a few new ones. During this period some seventy new species were described, which made in all about one hundred and twenty.

Nothing was known concerning the physiology of these plants and very little of the minute anatomy. When we consider that the scientific world was already familiar with the names of R. Hook, N. Grew, A. Loewenhoek, J. B. Triumfetti, and with the excellent work done with the simple microscope, we feel convinced that lichens must have been subject to a special neglect, leaving out of consideration the really excellent work of Tournefort.

Petiver[6] is supposed to have given the first description of a lichen from America (*Sticta damaecornis*).

III. PERIOD.

From Micheli (1729) to Weber (1789).

Micheli,[7] an Italian botanist, was the first to call attention to the inadequacy of grouping all lichens generically under the designation

[1] Plukenet, L. Phytographia. London. 1691. Almagestum Botanicum. London. 1696. Amaltheum Botanicum. London. 1705.

[2] Petiver, J. Gazophyllaceii Naturae et Artis Decas I.–X. 1703–1719. Musci Centuria X. London. 1695–1703.

[3] Vaillant, S. Botanicon Parisiense. Leide and Amsterdam. 1727.

[4] Ray, J. Synops. Meth. Stirp. Brit. London. 1690. 1696. 1724.

[5] Morton, J. Natural History of Northamptonshire. London. 1712.

[6] Petiver, J. Pterigraphia Americana. London. 1712.

[7] Micheli, P. A. Nova Plantarum Genera Juxta Tournefortii Methodum Disposita. Florence. 1729.

Lichen. This generic term became unsatisfactory in proportion as the number of known forms increased. There were, no doubt, botanists before Micheli who recognized this defect in lichen classification, but this author was the first to point it out to the botanical world. Micheli went, perhaps, to the opposite extreme and made too many subdivisions. He divided lichens into thirty-eight orders, basing this division upon the external appearance and consistency of the thallus, the position of the apothecia (*receptacula florum*), and the soredia (*semina*). Nineteen of these orders, representing one hundred species, were illustrated.

This step in advance was, however, more apparent than real, because of the fact that but little progress had been made in studying the morphology of these plants. It cannot be denied, however, that Micheli made good use of the simple microscope in the study of lichens.

The next prominent lichenologist was J. J. Dillen,[1] who made a considerable change in the system of Micheli. He grouped the lichens with mosses and subdivided them into three classes. These classes were again subdivided into orders, series and divisions, according to the structure of the thallus, and the structure and position of the apothecia.

After Micheli and Dillen other botanists did not hesitate to propose other arrangements, none of which were, perhaps, equal in value to those of the two eminent workers mentioned. These attempts were, however, indirectly productive of good results, because, in order to establish new systems, it was found necessary to make more careful observations in regard to the gross, as well as to the minute anatomy of the thallus and apothecia.

Hill,[2] who classed lichens with mosses, divided all the known species into six genera—*Collema*, *Usnea*, *Platysma*, *Cladonia*, *Pyxidium* and *Placodium*—whose limitations have been retained in part up to modern times. Adanson[3] classed lichens with fungi and separated them into nine genera. Linné's[4] system of lichens was in a certain sense retrogressive, since he grouped all these plants under the generic term *Lichen* (see Tournefort). This group was,

[1] Dillenius, J. J. Historia Muscorum. London. 1763.
[2] Hill, J. A. History of Plants. London. 1751.
[3] Adanson, M. Familles des Plants. Paris. 1763.
[4] Linné, C. Species Plantarum. Holmiae. 1753.

however, again subdivided into seven divisions, to which two more were added at a later period. Linné's system is of special importance, because it shows the first attempt at a natural arrangement. Beginning with *Graphis*, which he probably supposed to be the lowest form, he gives an ascending series terminating with *Usnea*, which is certainly a highly developed lichen. Nearly all authors of this period, subsequent to 1753, adopted Linné's system of classification.

The most remarkable characteristic of this period was the renewed uncertainty as to the position of lichens in the vegetable kingdom. Some authors classed them as fungi, others as algae, again as mosses. This doubt as to their true position continued to agitate the minds of botanists, and it has not been definitely removed at the present writing.

It would be impossible to review all the works on botany issued during this period which incidentally treat of lichens. As yet no specialists in the study of lichens had arisen; in fact, all the cryptogams were very much neglected. The study of higher plants of economic and of real or imaginary medicinal value absorbed the attention of botanists. The great systematists, in particular, took no interest in the lower forms of plant life. Linné designated lichens as "rustici pauperrimi," which may well be rendered "poor trash" of vegetation. In his "Species Plantarum" only eighty-six species are mentioned, although 170 were known at the time.

Progress in the study of the anatomy and physiology of lichens was especially slow and unsatisfactory although these divisions of botany were already known. Many botanists seemed possessed with the idea that there must be an analogy between flowering plants and lichens; hence efforts were made to find the male and female reproductive organs, fruit and seed. Wild and fantastic conjectures were made as to what structures in lichens should be compared to special organs in higher plants. Naturally, opinions differed very greatly. Micheli looked upon the soredia as "pollen dust," the apothecia were supposed to be the floral receptacles (*receptacula florum*), the spores the true "flowers." As already mentioned, this author also explained the asexual propagation of lichens by means of the soredia. Dillen, whose work was likewise of considerable importance, believed that the soredia constituted the pollen. His opinions in regard to the apothecia varied. At one time he supposed them to be the recepta-

cles for the seed, again the seed itself, or young plants, or even buds which served the purpose of reproduction.

Gleditsch, Scopoli and Linné believed that the apothecia were the male reproductive organs, while the soredia were the female reproductive organs. Necker[1] held the opposite opinion. Haller[2] accepted the theory of Micheli with regard to the functions of the apothecia and soredia. It scarcely need be stated that these various and varied opinions were based upon purely hypothetical assumptions and not upon direct observations.

In the pages devoted to the previous periods mention has been made of some of the uses to which lichens had been put in medicine and in the arts. In this period further efforts were made to widen their range of supposed usefulness. From the fact that scarcely anything was known of their anatomy and chemical composition, it is evident that many erroneous opinions must have been entertained in regard to their usefulness. Mead[3] recommended *Peltigera canina* as a cure for hydrophobia. Dried and finely powdered thalli of *P. canina*, mixed with finely powdered red pepper, formed the noted "pulvis antilyssus" (anti-hydrophobia powder) of the London Pharmacopoeia (1721 to 1788). In the history of the Royal Society it is recorded that several mad dogs, belonging to the Duke of York, were saved by this powder. The following is Dr. Mead's treatment in the case of hydrophobia. "The patient is bled and ordered to take a dose of powder in warm milk for four consecutive mornings; thereafter he must take a cold bath every morning for a month, and for two weeks subsequently three times a week." *Usnea barbata* was a favorite remedy for whooping cough; it was also recommended as an anodyne. (Dioscorides states that it was employed in certain diseases.) From its appearance it was supposed to promote the growth of hair. The yellow *Xanthoria parietina* was recommended in jaundice. The tonic and astringent properties of *Cetraria Islandica* were highly lauded by Ebeling.[4] Physicians and apothecaries of Iceland and Denmark recommended it in haemoptysis and phthisis. As an article of diet it had been long in use, not only for man, but also for domestic animals. "Iceland scurvy" was said to have been prevented by consuming a sufficient quantity of this lichen.

[1] Necker, N. J. Physiologia Muscorum. Mannheim. 1774.
[2] Haller, A. Historia Stirpium Indigenarum. Helvetiae Bernae. 1768.
[3] Mead, R. Poisons, 5th ed. 1818.
[4] Ebeling. Du Quassia et Cetraria Islandica. Glasgow. 1779.

IV. PERIOD.

From Weber (1779) to Wallroth and Meyer (1825).

In the previous periods lichens were classified mainly according to the differences in the form and structure of the thallus. In this period an attempt was made to classify them according to the "fruiting," that is, according to the form and structure of the apothecia. The first beginnings of this new departure, of course, commenced in the previous period, as we have already noted. Weber,[1] however, made the first intelligent effort to classify lichens upon this new basis. This author had formerly grouped all lichens in one order under "*Cryptogamia;*" he now arranged them under eight genera, *Verrucaria*, *Tubercularia*, *Sphaerocephalum*, *Placodium*, *Lichen*, *Collema*, *Cladonia* and *Usnea;* of these, the first four were based upon the characters of the apothecia alone; the others upon the characters of the thallus, as well as those of the apothecia. The majority of Weber's contemporaries adopted this new method of classification, with the result that entirely new systems were formed and new genera established. The following were some of the most active systematists: Willdenow,[2] who discovered the genus *Peltigera;* Schreber,[3] who proposed the genera *Physcia*, *Cornicularia*, *Sticta* and *Stereocaulon;* Humboldt,[4] who founded the genus *Opegrapha*. To Persoon[5] are credited the genera *Calicium*, *Sphaerophorus*, *Baeomyces* and *Placodium*. Although the majority of lichenologists followed in the footsteps of Weber, there were a considerable number who could not disengage themselves from the Linnaean influence. Of these we will mention only Hagen[6] and Jolyclerk.[7]

The Swedish lichenologist Acharius[8] began his study of lichens

[1] Weber, G. H. Wigger's Primitiae Florae Holsatiae. Kiel. 1780. Also, Spicilegium Florae Goettingensis. Gothae. 1778.

[2] Wildenow, C. L. Flora Berolinensis Prodromus. Berolini. 1787.

[3] Schreber, D. J. C. See Linné's Genera Plantarum, 8th ed., Vol. I. Frankfort-on-the-Main. 1791.

[4] Humboldt, A. von. Florae Freibergensis. Berolini. 1793.

[5] Persoon, C. H. Einige Bemerkungen über Flechten. Usteri neue Annalen der Botanik, 1: 1–32. 1794.

[6] Hagen, C. G. Tentamen Historiae Lichenum. Regiomont. 1782.

[7] Jolyclerk, N. Cryptogamie complete, ou description des plantes, dont les ètamines sont peu apparantes. Paris. 1799.

[8] Acharius, E. Nov. Act. Reg. Sc. Holmiae, **15**: 237–259. 1794. Nov. Act. Reg. Sc. Stockholmiae, **16**: 1795.

about 1793, and his great work was issued about seventeen years later (1810). This author divided lichens into three families according to the structure of the thallus: I. *Lichenes crustacei;* II. *Lichenes foliacei;* III. *Lichenes caulescentes.* Each of these families was again divided into several tribes (twenty-eight in all) according to the structure and position of the apothecia. He changed this system very materially at a later period.

It would be impossible to mention all lichenologists (including collectors) of greater or less note. However we may state that they made valuable collections at home and abroad and that their main desire was to determine old or new species. Little or nothing was done to ascertain the life-history of any of these interesting plants. Lamarck[1] described one hundred and fifty-seven species besides a number of doubtful forms. Jolyclerk mentioned and described three hundred and sixty-five species, which was a fairly complete list of all the lichens published at that time. It is, of course, impossible to know whether this was the actual number of species discovered on account of the numerous collections which were not published. There is also little doubt that many species published were duplicates. The most active collectors were at work in Germany, France, Austria, England and Switzerland. In 1802 it was admitted on good authority that in all about five hundred species of lichens were known.

In regard to the reproduction of lichens the controversy of the previous period continued; the question was still under discussion as to what lichen structures should be considered as the male and female organs. As in the previous period, these discussions and conclusions were mainly based upon hypothetical assumptions.

Hoffmann[2] agreed with Micheli that the soredia were the true seeds of lichens, but further believed that it was not improbable that the scutellae (apothecia) also contained seed; lichens were thus supposed to have a double means of reproduction. The true pollen (fertilizing substance) was supposed to be hidden in the lichen, and that fertilization took place internally during the early development of the plant.[3] Gärtner[4] perhaps came nearest the truth in regard

[1] Lamarck, M. de. Encyclopédie Méthodique. Botanique, 3: 470–508. Paris. 1789.

[2] Hoffmann, G. F. Commentatio de Vario Lichenum usu. Erlangen. 1786.

[3] Hoffmann's general illustrated works on lichens are: 1. Enumeratio Lichenum. Erlangen. 1784. 2. Descriptio et Adumbratio Plantarum. Classes Cryptogamica Linnaei quae Lichenes dicuntur. Leipzig. 1790–1801.

[4] Gärtner, J. De Fructibus et Seminibus Plantarum. 1788–1805.

to the function of the soredia. He believed them to be lateral branches or buds (*propagines*) and divided them into pulverulent (*pulverulentae*), filamentous (*scobiformes*) and leaf-like (*bracteolatae*). From this it is evident that his conception of soredia was much more comprehensive than that of the present day, as this author, no doubt, included the so-called isidioid outgrowths as well as the secondary thalloid branches. He stated that the *propagines* took their origin from the surface of the thallus and had the power of developing into new lichens without any preliminary changes. Schreber looked upon the soredia as gemmae rather than male reproductive organs, thus agreeing with Gärtner within certain limitations. Relhan[1] and others believed the apothecia were the female sexual organs and the soredia the male sexual organs. One of the most important works of the period was that of Hedwig.[2] He discovered the spermagonia, and not only gave very good descriptions of these organs, but of the apothecia, the spores and soredia as well. His descriptions were greatly strengthened by good illustrations. His conclusions were essentially as follows: The spermagonia which are the male reproductive organs develop first; subsequently the apothecia and soredia are developed upon them. He believed the apothecia with the spores to be the female reproductive organs, while the soredia constituted the fertilizing elements or the true pollen. As far as his conception of spermagonia and apothecia are concerned, we see that Hedwig anticipated the opinions held by some lichenologists of to-day. His theory with regard to the function of the soredia was, however, further from the truth than those of his predecessors.

We must also mention the rather unique experiments of De Candolle[3] illustrating the method in which lichens were supposed to take up their food-supply. This noted author employed a cochineal solution to observe the manner and rapidity with which various lichens absorbed this substance. As the result, he grouped lichens as to the manner in which he supposed them to absorb their food-supply. 1. Those which take their nourishment through the exterior. 2. Those

[1] Relhan, R. Flora Cantabrigiensis. Cantabria. 1785. Supplement I. 1786. Supplement II. 1788.

[2] Hedwig, J. Theoria Generationis et Fructificationis Plantarum Cryptogamarum Linnaei. 1784.

[3] De Candolle, A. P. Premier essai sur la nutrition des Lichens. Journal de Physique, de Chimie et d'Histoire naturelle, 47: 107. 1798.

which take their nourishment through a central canal. 3. Those which absorb through the exterior, but which also possess a central canal. As a whole, his explanations are very imperfect, which accounts, perhaps, for the fact that his treatise is at present almost entirely neglected.

Georgi[1] made some valuable chemical examinations of lichens and demonstrated the presence of oils, resins, gums, alkaline salts, silica, and other substances.

Acharius[2] seems to have been in great doubt as to the origin and structure of lichens. For a time he even questioned whether they were plants; that they, perhaps, belonged to the polyps. It was this doubt which led him to make more careful investigations concerning these plants. He made an especially careful study of the structure of the apothecia upon which his system[3] of classification is based. Though this system was doubtless an improvement on previous ones, it was subjected to severe criticism by Weber and other writers. This led Acharius[4] to improve and enlarge his former work. The illustrations of the structure of the apothecia and thalli are fairly good, but they indicate that he must have used poor microscopes. He gives only a few very crude illustrations of spores. One can readily understand that this system must, of necessity, be very deficient because no use was made of the spore-characters.

Sprengel[5] made an attempt to classify lichens according to the structure of the apothecia; it proved to be very unsatisfactory; it is evident at least, that this author had no definite ideas in regard to the "seed" and "fruit" of these plants. In a later work[6] Sprengel adopts the essentials of the system of Acharius and introduces German diagnoses of species.

Of the numerous lichenographers of this period there are ye three who deserve special mention, namely, Fries, Eschweiler and Feé. Fries[7] devoted his attention to the purely systematic con-

[1] Georgi. Chemische Untersuchungen einiger Flechten. Act. Acad. Scien. Petropol. pars. alt. 1779.

[2] Acharius, E. Anmärkinger rörande Lafarterne. Kongl. Vet. Acad. Nya Handl. 17: 1796. Prod. Lich. Suec. XVII. 1798.

[3] Acharius, E. Methodus Lichenum. 1803.

[4] Acharius, E. Lichenographia Universalis. Göttingen. 1810.

[5] Sprengel, K. Einleitung in das Studium der cryptogamischen Gewächse. Halle. 1804. English translation. London. 1807.

[6] Sprengel, K. Anleitung zur Kenntniss der Gewächse. 2d Ed. Halle. 1817.

[7] Fries, E. Conspectus Lichenum. K. Vetensk. Acad. Handl. 323–324. 1821.

sideration of lichens, without adding anything important to their morphology. His system of classification is not especially commendable, although it was for a time generally accepted. He divided lichens into two great divisions, the *Lichenes gymnocarpi* and *Lichenes angiocarpi*. The generic distinctions were based upon the form and structure of the apothecia and thallus. Of much greater value are the works of Eschweiler.[1] This author, whose early death was a great loss to lichenology as well as to botany in general, made a careful study of the apothecia and spores of lichens. He was the first to call attention to the different forms of spores, although his attempts at utilizing these spore-characters in his system of classification met with little success. Feé[2] in 1824 divided lichens into eighteen orders and sixty-six genera, seventeen of the latter being new. The characters of the thallus were utilized in the determination of the orders. His system was not favorably received. Fries and Feé will again be mentioned in the following period.

In America the work of collecting and naming lichens was also begun with great zeal, although the important work was not done until later periods. Many of the workers of this period devoted themselves to mere catalogueing. Michaux[3] published a short list of lichens (mostly new) collected in Carolina and Canada. Mühlenberg[4] published a list of Pennsylvania lichens. Eaton[5] published a list of North American lichens, likewise Torrey[6] and Halsey.[7]

In this period also appeared a number of monographs on lichens. The most noteworthy were those of Acharius who elucidated the genera *Arthonia*, *Thelotrema*, *Pyrenula*, *Trypethelium*, *Calicium*, *Glyphis* and *Chiodecton*. Floerke issued monographs on *Cladonia* and crustaceous lichens. Schaerer wrote a valuable treatise on the

Systema Orbis Vegetabilis. Part I. 1825. Lichenographia Europaea reformata. Lund. 1831.

[1] Eschweiler, Fr. G. Systema Lichenum. Nürenberg. 1824.

[2] Feé, A. L. A. Essai sur les cryptogames écareés exotiques officinales. Paris 1824.

[3] Michaux, A. Flora Boreali-Americana. 1803.

[4] Mühlenberg, H. Catalogue of the Plants of North America. Lancaster, 1813. Second Edition, Philadelphia, 1818.

[5] Eaton, A. Manual of Botany for North America. Albany. 1818.

[6] Torrey, J. A Catalogue of Plants growing spontaneously within 30 miles of New York City. Albany. 1819.

[7] Halsey, A. Synoptical view of the Lichens growing in the vicinity of the City of New York. Ann. Lyc. Nat. His. N. Y. 1: 3–21. 1824.

Gyrophorae of Switzerland. The more important monographs, however, were not issued until the following period.

During this period little or no progress was made in the knowledge of the anatomy and physiology of lichens. Although the compound microscope had been introduced, little use was made of it. This can readily be accounted for by the fact that the first compound microscopes were very imperfect and also because, being an innovation, they were regarded with distrust. Eminent opticians of the time boldly declared that the compound microscope could never excel the most perfect simple microscopes.

Strange opinions were entertained in regard to the origin of lichens. The belief in spontaneous generation and spontaneous transformation was general. It will be instructive as well as amusing to enter more carefully into some of the opinions entertained. Hornschuch[1] occupied himself with the problems of "generation" and "evolution." His opinions as far as they applied to lichens were as follows: "Algae, lichens and mosses may develop without seed from decomposing water. The decomposition of water induced by warmth and sunlight gives rise to the common ancestral type of the above vegetable forms. This ancestral type is a vegetable infusorium known as *Monas lens* (green substance of Priestley) which, when acted upon by light and air, undergoes an evolutionary transformation into alga, lichen and moss. Lichens are in reality mosses which have been checked in their evolution and might well be designated vegetable monstrosities. The apothecia (of lichens) are not the fruit, but rather the beginnings of a corolla, analogous to the flower of mosses (Moosröschen). The observations of Micheli in regard to the development of lichens from soredia are to be discredited since the discovery of the spontaneous generation of lichens." Sprengel[2] otherwise an accurate observer, believed that *Lecidea immersa* and *Monilia viridis* were evolved from chaotic masses due to the action of some force inherent in nature. The noted algologist Agardh[3] states that he observed the transformation of *Nostoc muscorum*, var. *lichenoides* into *Collema limosum*. Nees von Esenbeck[4] was wont to lead

[1] Hornschuch, Dr. Einige Beobachtungen über das Entstehen der Algen, Flechten und Laubmoose. Flora, 2: 140–144. 1819.

[2] Sprengel, G. Ueber Bau und Natur der Gewächse. Halle. 1812.

[3] Agardh, C. A. Dissertatio de Metamorphosi Algarum. Lund. 1820. Flora, 16: 17–41. (Beilage.) 1823.

[4] Esenbeck, Nees von. Handbuch der Botanik. 1820.

his pupils to an old castle in order to demonstrate *ad oculos* how the green substance of Priestley,[1] when occurring on rocks, will develop into lichens. These few citations will suffice to show that the science of botany was in its infancy.

Better work was being done in the chemical study of lichens. Here the investigations were limited to such lichens as had been found useful in the arts and in medicine. Most of the results obtained were published in the various chemical and pharmaceutical journals of the time. Those specially interested will find the references in various works on lichens.

The investigations in regard to the medicinal uses of lichens were not so extensive as in the previous period. During the wars of 1809–1815 fevers of all sorts were prevalent in military hospitals. Quinine, which was the popular remedy in all cases of fever, became very scarce because of the enormous quantities consumed and because of the commercial blockade of Europe. The Austrian government, therefore, offered a prize of five hundred ducats for the discovery of a cheap available substitute for quinine. Sanders,[2] who secured this prize in part, proposed *Parmelia parietina* as a substitute for quinine. It was soon found that the medicinal properties of this lichen were very unsatisfactory and the remedy was abandoned by physicians.

V. PERIOD.

From Wallroth and Meyer (1825) to Schwendener (1868).

This period marks the awakening of scientific lichenology as well as of scientific botany in general. It also marks the discovery of the "gonidia," which were destined to revolutionize the study and conception of lichenology. Likewise the spore-characters were beginning to be considered in the various systems of classification. We may well be astounded when we recollect that from Dioscorides to Wallroth, a period of two thousand years or more, the advance made in the exact knowledge of the anatomy of lichens was practically zero. The mere collection and arbitrary arrangement of plants do not give us any insight into their true nature.

[1] Wiegmann, A. F. Erzeugung mehrerer Gewächse aus der Priestley'schen grünen Materie. Flora, 4: 8–15. 1821.

[2] Sanders, G. C. H. Die Wandflechte (Parmelia parietina) ein Arzneimittel. Sonderhausen. 1815.

The first investigators who entered into a scientific study of lichens were Wallroth[1] and Meyer.[2] It is remarkable that the more important works of these authors should appear in the same year. Their object was not to collect and classify, but, rather, to study and compare the material already at hand. Of the two investigators it is generally conceded that Wallroth had the clearer insight into the nature of lichens, though in many respects he was not so careful an investigator as Meyer. The student of lichenology will however find, to his sorrow, that Wallroth's style is very involved. Each sentence contains a long series of parenthetical clauses which makes it very difficult to follow him. His terminology is also new and requires a special study. In spite of all these objectionable features, the work is certainly epoch-making. Wallroth was the first author to give us some knowledge of the vegetative propagative cells (Brutzellen = gonidia). He dwelt at considerable length on the "metamorphoses" of the thallus as well as on its general morphology. He demonstrated that some lichens were "homoemerous" and some "heteromerous" (these two terms are about all that have been retained of Wallroth's terminology). He made a careful study of the soredia and found that they consisted of gonidia enclosed by a delicate network (hyphae), and held the opinion that the gonidia, hence also the soredia, could develop into new plants. Under unfavorable circumstances the gonidium or soredium will not develop into a lichen, but simply form a green coating over the substratum. Though many of the conclusions were erroneous, it must be borne in mind that this was the first attempt at a scientific study of lichens. It is also much to be regretted that this author did not make use of the compound microscope; in some instances there is no evidence that he used even the simple lens.

Meyer's studies were perhaps more comprehensive than those of Wallroth. He entered into a careful consideration of the structure and metamorphosis of the thallus and apothecia, the gonidia and spores, the relation of lichens to the substratum, the growth and nutrition of lichens, etc. Meyer believed in the spontaneous generation (*generatio originaria*) of lichens which was stoutly denied by Wallroth. Wallroth believed that the gonidia and spores were the only reproductive organs of lichens.

[1] Wallroth, F. W. Naturgeschichte der Flechten. Frankfurt-am-Main. I. 1825. II. 1827.

[2] Meyer, G. F. W. Die Entwickelung, Metamorphose und Fortpflanzung der Flechten, etc. Göttingen. 1825.

We shall refer briefly to some of the other morphologists of this period. Mohl[1] made a careful study of the spores of cryptogams, including those of lichens. Körber[2] studied the gonidia and in the main verified the conclusions of Wallroth. He also made observations in regard to the reproduction and growth[3] of lichens. Körber's system of lichens[4] has no commendable features, his diagnoses being usually based upon macroscopic examinations. His orders, genera and species correspond to those of Massalongo. One thousand and fifty-one species of lichens are described as occuring in Germany and Switzerland. Two hundred and seventy-two species are described as new; from this it may safely be concluded that many species are only imaginary. The modern lichenologist will find it impossible to recognize many of the species from his descriptions. In passing it may be stated that this criticism will apply to the greater number of systematic works issued during this period as well as in the previous periods. The results of Massalongo's[5] studies were of considerable importance. This author concluded that the spore-characters, as well as the form and structure of the apothecia and thallus, should be considered in the establishment of the genera. It is, however, generally conceded that many of his species and some of his genera were poorly founded. Fries[6] also recognized the importance of spore-characters in generic distinctions and in addition considered the form of the spermatia and sterigmata of importance in classification. It was, however, left to Stitzenberger (91) to point out the real value and significance of the spore-characters in the classification of lichens. He believed that in general it was necessary to consider the number of septa in the spores as well as their direction. Lichens with spores differing in the number of septa are not to be included in the same genus. He believed that the spores were equal in importance to the flowers and

[1] Mohl, H. Einige Bemerkungen über die Entwickelung und den Bau der Sporen der cryptogamischen Gewächse. Flora, **16**: 32–46, 49–63, 65–73. 1833.

[2] Körber, G. W. De Gonidiis Lichenum. Berlin. 1839.

[3] Körber, G. W. Bemerkungen über individuelle Fortpflanzung der Flechten. Flora, **24**: 6–14. 17–32. 1841.

[4] Körber, G. W. Systema Lichenum Germaniae. Breslau. 1855. Parerga Lichenologica. Breslau. 1865.

[5] Massalongo, A. Recerche sull' anatomia dei Licheni crostosi. Verona. 1852. Memoiree Lichenografiche. Verona. 1853. Monografia dei Licheni blasteniospori. Venice. 1853.

[6] Fries, Th. M. Genera Heterolichenum Europaea recognita. Upsala. 1861.

fruit in higher plants; the spermatia were not looked upon as being of any special significance in the classification of lichens. The English lichenologist, Mudd,[1] emphasized the importance of the spore-characters and likewise considered the spermagonia as being of only secondary importance.

At this time the arrangements proposed by Massalongo and by Körber received general recognition. Now, however, appeared an investigator, an able systematist, who, in a certain sense, revolutionized the classification of lichens. Nearly all previous lichenologists arranged them beginning with the highest forms and working toward the lowest. Nylander,[2] however, had an entirely different conception of how these plants should be arranged. He believed that they presented a double affinity; on the one hand they showed a close resemblance to fungi, on the other hand to algae. In his system he arranged lichens beginning with those forms most nearly resembling the algae, thence proceeding to the highest forms as *Sticta*, *Parmelia* and allied groups. From these highest forms he proceeded to the forms most nearly resembling the fungi. From this it would seem that he had the first somewhat definite conception of the true nature of lichens. The most remarkable thing in his system is the contempt with which he treated the spore-characters in the limitation of genera and tribes, restricting them to specific distinctions. He believed that the form, structure and composition of the thallus, apothecia and spermagonia must form the generic characters. Chemical reactions of the thecium, especially with iodine, were considered of much importance. Nylander also considered the color and structure of the gonidia. He published a list of all the known lichens, which included 1,348 species, 298 of which were described as new.[3]

We have mentioned the leading systematists of the period. We shall now hastily review the works of the leading morphologists of this time. It must not, however, be forgotten that many of the systematists also devoted some attention to the morphology of lichens, but only in so far as it was necessary to enable them to arrange the plants according to some preconceived system. No advanced work was done by them; this was left to the investigators who believed

[1] Mudd, W. A Manual of British Lichens. Darlington. 1861.

[2] Nylander, W. Syn. Meth. Lichenum. Paris. 1858.

[3] Nylander, W. Enumération générale des Lichens avec l'indication sommaire de leur distribution geographique. Cherbourg. 1858.

that a thorough study of the life-history, morphology and physiology of plants was necessary before they could be properly classified.

Itzigsohn will be the first to receive our attention. His opinions varied in regard to the spermagonia (38). He was inclined to believe that they were parasitic fungi, abnormal spore-organs, apothecia or even parasitic lichens. Later (41) he expressed it as his opinion that the spermagonia were the antheridia of lichens analogous to those of mosses, and the spermatia, the spermatozoa. Still later (42) he states as the result of the study of *Parmelia parietina* that the gonidia "of lichens which are reproduced from gonidia," are the female organs and the spermatia the male organs, and that fertilization of the gonidia takes place outside of the thallus. *Pleurococcus*, *Ulothrix*, and other algae were supposed to be unfertilized gonidia enabled to lead an independent existence.

Of much more value were the investigations of Tulasne. He gave the first somewhat exact description of the morphology of many lichens (97). Especially valuable are the accompanying illustrations of sections of the thallus, apothecia and spermagonia. This author proposed the term spermagonium for the small structures upon the thallus, and spermatia for the minute rod-like bodies within the spermagonium. He was also the first to demonstrate that the spermatia are formed on sterigmata, and that they do not have autonomous movement. As to the function of the spermagonia he believed that they were peculiar reproductive organs, physiologically closely related to the apothecia. He was also the first to call attention to the "pycnids" and the "stylospores."

Lindsay likewise did some excellent work in the morphology of lichens. In his prize essay he presents a communication in regard to the morphology of spermagonia and pycnidia. As to their function he is inclined to the belief that they are analogous to male reproductive organs. Lindsay has also given us a very interesting and popular history of British lichens.[1] This excellent little work contains good illustrations showing the morphology of the thallus, apothecia and spermagonia; it gives the history of lichenology, the uses of lichens and diagnoses of the more prominent forms.

Schwendener, whom we shall mention more particularly in the next period, now began his interesting studies of lichens (79). He made a careful research on the morphology of the majority of known

[1] Lindsay, W. L. A popular History of British Lichens. London. 1856.

lichens, doubtless the most comprehensive study of the subject ever undertaken up to this time. Especially valuable are his observations in regard to the growth of lichens. His careful study of the anatomy of these plants contributed very valuable aid to the future classification of lichens. It is, however, especially interesting to note that at this time (1858–1863) he was convinced that the gonidia developed from the hyphae, as branches develop from the side of a stem. In this he agreed with Bayrhoffer (5, 5a) and Speerschneider (84). In the next period we shall find that he changed his opinions as far as gonidia were concerned. Not much can be said in favor of the illustrations accompanying Schwendener's communications.

Another important work of the period was that of de Bary.[1] In the work cited, this author gave a clear and concise description of the minute structure of lichens. In many respects it resembled the work of Schwendener; in fact, a number of the illustrations were taken from his work. De Bary gave a very comprehensive description of the morphological and anatomical relations of the crustaceous lichens. We cannot enter into a full discussion of de Bary's work; one opinion expressed by this author should, however, be referred to in particular, since it has bearing upon the conclusions arrived at in the next period. De Bary believed that some of the gelatinous lichens (*Ephebe*, etc.) were either perfect or mature states of plants whose immature states are recognized as forms of *Nostoc*, *Chroococcus*, etc.; or that these organisms are true algae, attacked by certain ascomycetes, whose hyphae penetrate the algae and form the lichen-thallus. From this we see that De Bary was the first author to hint at the true nature of lichens. He also issued a very valuable communication in regard to the development of certain lichen-spores (22).

Considerable progress was also made in the chemical study of lichens. Various substances peculiar to lichens were discovered, such as cetrarin, variolin, orcin, erythrin, picroerythrin, evernin, physodin, besides various acids, as cetraric acid, evernic acid, and fatty acids. The alkaloids and acids discovered proved so varied and variable that Schunk[2] came to the conclusion that one

[1] De Bary, A. Morphologie und Physiologie der Pilze, Flechten und Myxomyceten. Leipzig. 1866.

[2] Schunk, E. Einige Bermerkungen über die von Stenhouse in der Rocella tinctoria and Evernia prunastri entdeckten Substanzen. Erdmann's Journal für practische Chemie, **46**: 18–30. 1849.

and the same lichen would yield different chemical compounds depending upon a difference of locality and substratum. French and Scandinavian chemists employed lichens (especially *Cladonia rangiferina*) in the manufacture of alcohol.

These chemical investigations were primarily conducted with a view to improve the dye industry dependent upon the various coloring substances derived from lichens. France, more than any other country, improved upon the methods of extracting the dye, as well as of applying it. Orseille was especially recommended in dyeing woolen and silken goods. Innumerable methods for extracting the dye as well as for improving its durability were employed. Some of these methods were patented.

Lichens also found a wider use as an article of diet. *Cetraria Islandica*, because of its high percentage of lichen-starch (lichenin), was especially recommended as already mentioned. The inhabitants of Iceland, Norway and Sweden mixed this lichen with various cereals and mashed potatoes, from which an "uncommonly palatable and healthful bread was prepared." Sir John Franklin and his companions made use of this lichen during their Arctic voyages. Its use to prevent the peculiar disease known as "Iceland scurvy" continued. In general, however, it may be stated that lichens were used as an article of diet only in the case of a famine or in those countries where the cereals are not abundant, principally because all lichens contain a bitter principle, which is very disagreeable to the taste and difficult to remove and which has a deleterious effect upon the digestive tract, producing a form of intestinal inflammation.

As to the use of lichens in medicine it was found that they were not reliable, and other drugs soon supplanted them. They were, however, recommended as an article of diet for convalescents, especially "Iceland moss" (*Cetraria Islandica*). The peasantry of various countries still believe in the healing properties of various lichens. We have already mentioned *Peltigera canina*. In Sweden *Peltigera aphthosa* was boiled in milk and given to children afflicted with "thrush." Decoctions of various lichens (especially *Parmelias* and *Cladonias*) were employed in intermittent fevers. The purgative properties of most lichens (particularly the *Umbilicarias*) are well known; various species of *Gyrophora* and *Umbilicaria* were the cause of severe illness among members of the Franklin expedition.

VI. PERIOD.

From Schwendener (1868) to Reinke (1894).

This is by far the most important period in the entire history of lichenology. It is marked by the recognition of the true nature of lichens and their classification as modified fungi. Since most of the literature of this period is readily accessible I shall not review it at length and shall limit myself to a very brief outline of the work done during this period, mentioning only a few of the leading investigators.

The most important work of the period was the discovery of the dual nature of lichens. That is, a lichen consists of a fungal and an algal portion associated in an intimate organic union. Although Schwendener is generally credited with having made known this discovery, it must not be forgotten that the preparatory work was done in the preceding period; also that Schwendener did not at first believe in the dual nature of lichens. Not until the year 1868 (79) did he express the opinion that the gonidia of various lichens corresponded to certain low forms of algae. His conclusions of that time may be summarized as follows:

1. There is no direct proof of any genetic relation between the gonidia and the hyphal elements.

2. The cell-walls of the gonidia have a different chemical behavior from the membranes of the hyphae; the former react similarly to those of algae, the latter similarly to those of fungi.

3. As to structure and development the various forms of gonidia correspond to different forms of algae. The resemblance is so close that in many cases a given isolated gonidium cannot be distinguished from the corresponding alga. The algal types are as follows:

(a) The majority of heteromerous lichens (*Usnea*, *Bryopogon*, *Evernia*, *Physica*, *Anaptychia*, *Imbricaria*, *Parmelia*, etc.), contain species of the algal genus *Cystococcus* Naeg. (*C. humicola* and related forms).

(b) Some other heteromerous lichens contain species of *Pleurococcus* Menegh. (*P. vulgaris* and related forms).

(c) In *Roccella* we find the algal genus *Exococcus* Naeg.

(d) *Omphalaria* and other lichens with blue-green gonidia contain various representatives of the Chroococcaceae as *Gloeocapsa*, *Chroococcus*, and perhaps other related forms.

(e) The Collemaceae are associated with *Nostoc*.

(f) *Ephebe* and related genera with *Stigonema*. (*Ephebella Hegetschweileri* with *Scytonema*.)

(g) *Hormogonium* and *Cystocoleus* are associated with an alga belonging to the Confervaceae.

(h) *Graphis*, *Opegrapha* and related forms are associated with *Chroolepus*.

4. The development of the spore never proceeds further than the protothalloid stage, perhaps because of the absence of the requisite algae.

5. There is a great similarity between the lichens and the pyrenomycetous fungi.

Schwendener issued a communication on the algal types of lichens in the following year (81). It is accompanied by colored plates illustrating most of the lichen-algae. Famintzin and Baranetzky (23, 24) demonstrated experimentally that the gonidia of heteromerous lichens, such as *Physcia*, *Evernia*, *Cladonia* and *Peltigera*, as well as some of the gelatinous lichens, as *Collema*, are capable of developing apart from the thallus, even producing zoospores like the unicellular algae. In spite of this fact these investigators concluded that the gonidia were not algae, and further expressed the opinion that perhaps many of the unicellular algae were simply free lichen-gonidia.

Woronin (103) demonstrated that the gonidia of *Parmelia pulverulenta* never produce hyphal filaments, but always develop into new gonidia; or, what is the same thing, the free gonidium which is neither more nor less than a species of *Cystococcus* develops into new colonies of algae. He thus opposes the view held by Baranetzky and Famintzin and favors the theory of Schwendener. Rees (74) demonstrated that the hyphae developed from the spores of *Collema glaucescens* will not mature unless associated with *Nostoc lichenoides*; in the absence of such an association the young hyphae soon perish. A few years later Bornet (15, 16) isolated and determined specifically the algae which enter into the composition of a large number of lichens. He also described the method by which the hyphae envelop the algae, as well as the mutual benefit derived from the intimate association of algae and fungi. Similar observations were made by Treub (94).

These and other experiments demonstrated beyond a doubt the

dual nature of lichens. They also demonstrated that this association was not like that of ordinary parasitism, but rather formed a union for mutual benefit, thus enabling these plants to exist where neither of the components could exist alone. This association was known as consortism (Reinke), or symbiosis (de Bary).

There were also a large number of investigators engaged in the study of the morphology as well as the physiology of particular groups of lichens as well as of lichens in general. We will mention a few of these. Stahl (89, 90) made a special study of the spermagonia. His conclusions were that in *Collema* the spermatia are the male reproductive organs. The female reproductive organ known as the carpogone after being fertilized by the spermatia develops into the apothecium. It is interesting to note that this form of sexual reproduction was observed only in *Collema*. Recently Sturgis has apparently verified Stahl's results (93). Further investigations are necessary to establish Stahl's theory. A number of investigators have demonstrated that the spermatia will develop a hyphal network, even developing new spermagonia. This would seem to prove that spermatia are true spores instead of sexual organs. The most important work in regard to the physiology of lichens was done by Jumelle (44). This author gave us the first reliable results of observations made on the exchanges of gases in fruticose and foliose as well as in crustaceous lichens. He found that the exchange of O for CO_2 is independent of the substratum and dependent upon sunlight and moisture, and also that this gaseous exchange varies greatly in different lichens. An excess of moisture reduces carbon-assimilation. Respiration in some lichens still goes on at very low temperatures, — 10° to — 40° C. Lichens can also resist much higher temperatures than phanerogams. For instance, respiration was still active when the lichen was exposed for one day to a temperature of 45° C., three hours at 50° C. and one-half hour at 60° C.

Among the systematists we will mention Tuckerman,[1] who considered Körber's system the most useful and adopted it in his classification of the North American lichens; his diagnoses are carefully given, accompanied by spore-measurements. With Nylander he considered the spermagonia of great importance in classification. A number of new species were described. He also issued a work

[1] Tuckerman, E. Synopsis of North American Lichens. Part I. 1882. Part II. 1888.

on the genera of lichens and their relationships,[1] which is, however, unsatisfactory, because the author did not seem to have any clear conception of genera. Leighton's manual of English lichens[2] has no commendable features; the spore measurements are quoted; his diagnostic terminology is a peculiar mixture of English and Latin. Körber's and Nylander's methods of classification were referred to in the previous period. Hué published a list of exotic lichens,[3] from which it is safe to estimate that nearly five thousand species and varieties were known at the time. Of this number some are no doubt duplicates. It must be remembered also that a host of varieties, sub-varieties and forms were described. It is at present impossible to state the actual number of authentic species.

Schwendener and his followers uniformly agreed to classify lichens as fungi. To this the systematists objected very strongly. Naturally, they also objected to Schwendener's theory as to the true nature of lichens. In fact, all through this period we find the morphologists and physiologists pitted against the systematists; the former earnestly endeavoring to get at the life-history of the various lichens, the latter refusing to recognize the discoveries made by the former and continuing the work of arbitrary classification. The work of Jatta[4] deserves special mention. He precedes the descriptions of the lichens of southern Italy by a discussion of the anatomy and biology of lichens, and adds a number of colored plates illustrating the principal morphological characters. It is not complete, but it is a work contributing much to the scientific evolution of lichenology.

The use of lichens in the arts, in medicine and in the household was still continued. Great improvements were made in the method of using the various lichens in the dye industries. For further particulars the student is referred to three little works on the uses of lichens by Magnin[5], Henneguy[6] and Porcher[7]. As far as the medicinal uses of lichens are concerned we find that the allopathic school

[1] Tuckerman, E. Genera Lichenum. Amherst. 1872.

[2] Leighton. W. A. The Lichen-flora of Great Britain, Ireland and the Channel Islands. Shrewsbury. 1879.

[3] Hué, A. M. Lichenes Exotici. Paris. 1892.

[4] Jatta, A. Monographia Lichenum Italiae meridionalis. Trano. 1889.

[5] Magnin, Dr. A. Les Lichens utiles. Lyon. 1877.

[6] Henneguy, Dr. F. Les Lichens utiles. Paris. 1883.

[7] Porcher, F. P. The Medicinal, Poisonous and Dietetic Properties of the Cryptogamic Plants of the United States. New York. 1854.

has practically abandoned them as being too unreliable in their effects. In Bartholow's Materia Medica (1884) we find that only *Cetraria Islandica* is recommended to be given as a stomachic tonic, "but only to be prescribed when the more efficient remedies are not well borne." The homeopathic school of medicine still recommends certain lichens in a few diseases, for example, *Sticta pulmonaria* in lung troubles. Other lichens are given in whooping-cough, etc.

VII. PERIOD.

From Reinke (1894) to the Close of 1896.

I may be justly criticised for recognizing this as a period, since Reinke's propositions have not been generally accepted as correct. It can not, however, be denied that his conclusions are based upon sound argument and should, therefore, mark the beginning of the period in which lichens are recognized as a distinct class of plants; such recognition being based upon physiological considerations. In his article on "Die Stellung der Flechten im Pflanzensysteme" (75, III) Reinke endeavors to demonstrate that lichens are autonomous structures. He recognizes and admits all the facts established by Schwendener and his followers, but maintains that lichens are physiologically as well as morphologically sufficiently distinct from both fungi and algae to be recognized as a distinct class. Although the lichen-algae may be cultivated artifically this does not indicate that lichens should be considered as fungi parasitically associated with algae. The fact remains that when either of the symbionts is removed the lichen no longer exists; its autonomy is destroyed. The difference between the school of Schwendener and that of Reinke is principally a difference of opinion as to what constitutes autonomy. Tubeuf (96) states that in mutualism we have a union of fungus and alga which produces an individual wholly different from either of the components and *entirely distinct* as to *form*, *requirements* and *conditions* of life. This intimate nutritive association of two or more originally distinct organisms, which is typically met with in lichens, Tubeuf designates as *individualism*. According to this definition lichens should, doubtless, be treated as a distinct class.

It will be remembered that Tuckerman and others of the previ-

ous period maintained that lichens formed a distinct class of plants. But Tuckerman and Reinke had entirely different conceptions as to the nature of lichens. The former did not believe in their dual nature and, therefore, could not form any true idea as to the relation they bear to other groups of plants, the fungi and algae in particular. For that reason we are justified in stating that Reinke was the first to indicate the true position of lichens in the vegetable kingdom.

Lindau (53) is opposed to Reinke's views and strenuously upholds the theory of Schwendener. As has already been indicated, the future must decide which theory will prevail.

Reinke also pointed out the polyphyletic origin of lichens (75, III, IV). The various groups (usually generic) of lichens are derived from different fungal ancestors. Usually several fungal ancestors have become associated with the same algal type, or the same fungal type may have become adapted to different algal types. Reinke has proposed a system based upon this polyphyletic relationship, which, when more perfected, will form the first approximately natural system of classification for lichens. As this author states, to study the exact phylogenetic relation of lichens to fungi and algae, is one of the important works of the future.

Fünfstück (32) has investigated the fatty secretions found within crustaceous rock lichens. His conclusions are briefly summarized as follows: Calcivorous crustaceous lichens vary greatly as to the depth to which they penetrate the substratum; the endolithic forms have a deficient algal layer as compared with the epilithic forms; the fatty deposition increases with the increase of the gonidial layer, but has no genetic relation to it; the fatty substance is deposited in the hyphae lying within the substratum; fat is deposited only in lichens growing upon a substratum bearing carbonates; the formation of the fatty substance is very likely initiated by the decomposition of the carbonates.

Lindau (54) has also issued the first of a series of communications on the morphology and physiology of lichens. Part 1 treats of the growth and mode of adhesion of crustaceous bark lichens. He concludes that the hyphae never penetrate the intact cells of the substratum. He has also considered the question whether lichens have or have not an injurious effect upon trees (54). He comes to the conclusion that they have no injurious effect upon trees growing under normal conditions. Only when the trees are growing in poor

soil, or when too closely crowded, can a profuse development of lichens have an injurious effect.

Of the systematists of this period we will mention only Crombie.[1] In his classification of British lichens this writer has adopted Nylander's system. He does not recognize Schwendener's theory and divides the lichen-algae into gonidia, gonimia and gonidimia. His diagnostic terminology is that peculiar mixture and combination of English and Latin so much employed by English systematists of this as well as of the preceding period.

We shall conclude this historical review with a brief reference to fossil lichens; so far there is no reliable record of any such remains. There is, however, little doubt that lichens existed during former geologic ages. No records are left for the same reason that we have few authentic records of fossil algae and fungi, that is, lichens are not sufficiently resisting to become fossilized. Excavations of prehistoric cave dwellings (Germany) have revealed the presence of lichens (*Cladonia rangiferina*) among the bones of various animals and the stone implements, which would indicate that man of that early period had already made some economic uses of them.

[1] Crombie, British Lichens, I., 1895.

CHAPTER II.

SYMBIOSIS.

INTRODUCTION.

Since Schwendener's epoch-making researches, which have fully established the dual nature of lichens, other investigators have made valuable discoveries in regard to the nutritive interdependence of different organisms. The student will readily comprehend the important bearing this subject has upon the study of lichens. A general consideration of the subject of symbiosis will enable us to have a more definite opinion in regard to the life-history of the individual lichen.

The study of the symbiotic relationship (consortism of Reinke, symbiosis of De Bary) of different organisms is of comparatively recent origin. As generally admitted, the phenomenon of symbiosis was first explained by De Bary in the year 1879[1]. By symbiosis this author understood a form of nutritive commensalism or consortism of different organisms which proved mutually beneficial. It was, therefore, placed in opposition to parasitism, which is a form of commensalism in which one of the organisms is benefited at the expense of the other. Within recent years the term symbiosis has been used to designate all forms of commensalism, whether parasitic, indifferent or mutually beneficial. It is in this broader sense that the term is here used.

We shall now briefly consider the gradation from antagonistic symbiosis (parasitism) to the most highly developed mutualistic symbiosis (individualism) as we find it in lichens.

I. ANTAGONISTIC SYMBIOSIS. (PARASITISM.)

It is assumed that the student is sufficiently familiar with the antagonistic symbiosis of fungi with higher plants as well as with ani-

[1] The phenomenon of symbiosis had, however, been previously explained by Reinke. He used the term "consortism" to distinguish this relationship from true parasitism. His views are explained in the following publications:

Reinke, J. Göttinger Nachrichten, p. 100. 1872. Reinke, J. Morphologische Abhandlungen. Leipzig. 1873. Reinke and Grisebach, A. S. Oersted's System der Pilze, Lichenen und Algen. 1873.

mals to require no further elucidation of the subject here. Another and but little known phase of this subject is the antagonistic symbiosis of fungi with lichens, and of lichens with lichens, and with mosses. We shall now consider these relations somewhat more in detail.

1. ANTAGONISTIC SYMBIOSIS OF FUNGI WITH LICHENS.

There are no natural reasons why this form of symbiosis should not be of frequent occurrence, although no special study has been made of the subject. It is also very likely that many so-called parasitic lichens are in reality parasitic fungi. A number of herbarium specimens described as parasitic lichens proved, on closer study, to be fungi; in no case could a thallus be detected. It was also evident that these parasitic fungi (Ascomycetes) had an injurious effect upon the algae of the lichen-thallus, as they were nearly all destroyed in the immediate vicinity of the fungus. As far as it has been possible to observe, these parasitic fungi usually occur on the upper surface of the lichen-thallus, quite rarely on the lower surface, as in *Endocarpon miniatum*. It is a comparatively difficult matter to study the organic union of the symbionts, since the hyphal threads of both are very similar. This difficulty we do not encounter where fungi are parasitic upon higher plants. I have repeatedly made careful sections through host and parasite and employed various staining methods, but did not succeed in demonstrating definitely that the hyphal network of the supposed parasite was or was not continuous with that of the host. By crushing methods, assisted by various alkaline solvents, one can readily separate the two symbionts, but this is not incontestible evidence that they were not organically united. This difficulty of investigation also applies to the so-called pycnidia and spermagonia. But since we are certain that there are ascomycetous fungi parasitic upon lichens, so, likewise, in regard to spermagonia and pycnidia it is reasonable to assume that they are parasitic fungi, especially since it has not been conclusively demonstrated that they are male reproductive organs. It is also reasonable to assume that the parasitic fungi of lichens are morphologically and physiologically different from the same forms of parasitic fungi of higher plants, a variation induced by a marked difference in the substrata. Even leaving out of consideration the spermagonia, which we shall discuss more in detail in another chapter, parasitic fungi are

quite common upon lichens. Although most of the fungi parasitic upon lichens belong to the Ascomycetes, there are also a few from other groups. Not unfrequently some species of *Mucor* entirely destroys the lichen-thallus; it is, however, quite probable that this occurs only when the vitality of the lichen is very much reduced and the plant exposed to a high degree of moisture.

The method of infection is much the same as in higher plants. A spore of the parasite falls upon the surface of the thallus, where it develops a mycelium which destroys the hyphal tissue of the host, or, at least, very materially retards growth, so that in time the parasite is more or less completely enclosed by the upper layers of the lichen-thallus. The line of demarcation between host and parasite is sometimes abrupt and distinct, owing to a difference in color, but, as already indicated, it is very difficult to demonstrate the relation of the hyphae of the parasite to those of the host. It is very desirable that this form of symbiosis should be investigated more carefully. Some experiments solving the problem of the true physiological relationship of fungal parasites to lichen-hosts would be especially interesting.

Physarum mucoroides, a Myxomycete, occurs quite constantly upon *Pertusaria communis* and *Sticta globifera*; other Myxomycetes occur less constantly.

2. ANTAGONISTIC SYMBIOSIS OF LICHENS WITH LICHENS. (SYNTROPHY.)

That different species of lichens should occur in symbiotic association is not surprising when we consider the fact of their close proximity in nature; there is a continual struggle for space. Very frequently we find foliose or fruticose lichens spreading over and crowding out the crustaceous forms. We also find that one form of crustaceous lichen will encroach upon another form and gradually cause it to disappear This is readily understood in the case where one lichen is of more rapid growth than another. As Minks has shown in his communication on the syntrophy of lichens (65, 67), one species of crustaceous lichen may form the lower thalloid portion, while a second parasitic species may develop the apothecia. Not only one, but several, different species may form successive layers upon the lowermost host-species. It frequently happens, doubtless, that the host-lichens are sooner or later entirely destroyed, in which case we can find only the parasitic form growing upon the fragmentary remnants

of the host or hosts. Minks is also inclined to believe that the so-called "protothallus" is simply the remnant of a host-lichen. Although it is questionable whether syntrophy is of as frequent occurrence as Minks supposes, there is no doubt that it does occur, not only among the lower lichens, but among the higher forms as well. I have found a species of *Lecanora* growing upon a *Collema*-thallus. There are many undecided problems connected with this form of symbiosis. No one has as yet been able to observe the complete course of development of this form of parasitism; that it is parasitism is quite certain. I have not adopted the term syntrophy proposed by Minks, since it indicates nothing which is not already implied by the term parasitism or antagonistic symbiosis.

3. ANTAGONISTIC SYMBIOSIS OF LICHENS WITH MOSSES.

According to Bonnier (11) certain lichens, *Lecidea vernalis* in particular, live parasitically upon the protonema of mosses. This author has made numerous culture experiments to verify his observations. He placed moss and lichen spores upon sterilized substrata, where their development could be readily observed. It was found that the hyphal filaments formed a mycelium about the protonema, even entering the cells, where they formed a dense network, causing the protonemal cell to become considerably enlarged. It is evidently a form of antagonistic symbiosis, because the protonema is killed in a short time. Bonnier has observed this antagonistic symbiosis of lichens in different genera of mosses. Lichens also occur parasitically upon the leaves and other parts of mosses, as well as upon higher plants. Practically nothing is known of the life-history of lichens parasitic upon higher chlorophyll-bearing plants, although they are numerous and have been known for a long time. They are mostly low forms of lichens and occur principally in tropical regions. Many of the occurrences of supposed antagonistic symbiosis require further study. There is little doubt that many of the injurious effects supposed to be due to antagonistic symbiosis of lichens is, in reality, caused by mechanical interference. For instance, a lichen spreading over a moss, which is of frequent occurrence, cuts off sunlight as well as air, thus having an injurious effect in an indirect way. It is generally admitted by the leading investigators that the lower forms of lichens, in particular, take very little

nourishment from the substratum (host-plant), at least not sufficient to produce any injurious effects. (For further particulars see 11.)

II. NUTRICISM.

This establishes a connecting link between antagonistic symbiosis and mutualistic symbiosis. Tubeuf defines it as that form of symbiosis in which one symbiont nourishes the second symbiont without receiving any food supply in return; that it is, so to speak, a one-sided symbiosis. Tubeuf recognizes two forms of nutricism. In the first the saprophytic fungus living in contact with the growing root-tips of higher plants supplies soluble organic food substances, the fungus acting in the manner of a transfer agent. In the second the fungus lives within the root-cells of the host-plant. The author admits that the fungus is at first nourished by the host, but that it finally dies and is absorbed. The second form is undoubtedly mutualistic symbiosis, as will be explained in the next chapter. I will therefore, limit myself to a discussion of the first case; it must be remembered that it is very frequently difficult to decide what is merely nutricism and what is mutualistic symbiosis.

The most common form of nutricism is met with in the occurrence known as mycorhiza (fungus-root). This is the association of a fungus and the root of some higher plant. It is frequently met with among the Cupuliferae growing in humus-bearing soil. The hyphal fungus forms a network about the young root-tip of the growing tree; its function is to supply the tree with organic food substances taken from the soil; in a certain sense it supplants the function of the hair-cells which are wanting in the mycorhiza. The fungus does not receive any marked benefit from this association, but it has been conclusively proven, experimentally, that the tree is very materially benefited. The hyphae of the fungus always remain on the outside of the root and this form is, therefore, known as ectotrophic mycorhiza. In the endotrophic mycorhiza of Orchids the fungus enters the parenchyma cells of the root where the hyphae develop a mycelial network; too little is known concerning this phenomenon to give any correct explanation of it; it is at present impossible to state whether it is a case of antagonistic symbiosis, nutricism or mutualistic symbiosis. In regard to the ectotrophic mycorhiza we are certain that it is not a form of antagonistic symbiosis.

In *Cycas revoluta* we find a form of symbiosis which is un-

doubtedly nutricism, but it differs from that above described in that the host-plant acts as the transfer agent. It is found that in the majority of cultivated *Cycas* species there are numerous tubercular outgrowths from the roots which usually contain a species of *Nostoc* between the cells of a specialized parenchyma. This is evidently not a form of parasitism, as is shown by the fact that the cycads bearing the greater number of tubercles are in no wise injuriously affected. Neither has it been proved that the host receives any material benefit from this association. There is, however, no doubt that the *Nostoc* is dependent upon the host for its food supply. For the time being it may be looked upon as nutricism.

There are numerous other forms of symbiosis which come under the head of nutricism, but sufficient has been given to explain the subject and to prepare the way to a better understanding of mutualistic symbiosis.

III. MUTUALISTIC SYMBIOSIS.

In mutualistic symbiosis host and parasite form a biological union resulting in mutual benefit. On closer examination two forms may be recognized. In one the symbionts (there may be two or more) are not wholly dependent upon each other for their existence; that is, the symbionts are all capable of leading an independent existence. In the second form at least *one* of the symbionts is absolutely dependent upon the symbiotic association. The former Tubeuf designates as *mutualism*, the latter as *individualism*.

1. MUTUALISM.

This form of symbiosis is of comparatively recent discovery. Frank, more than any other investigator, has given this subject his attention, especially its occurrence among the leguminous plants. In the Leguminosae we find the constant occurrence of certain bacteria (rhizobia) within the root-parenchyma causing the development of tubercles. It is, doubtless, a form of mutualism, although Tubeuf considers it a case of nutricism. The bacteria which infect the root-cells and cause the development of the tubercles are dependent upon the host for their food supply. They are even excessively supplied with nourishment, as is indicated by their enormous development. The host in return receives the nitrogenous compounds formed by the bacteria in the process of binding the free nitrogen of the air. It

is true that the benefit received by the host is far greater than that received by the infecting bacteria, but it is nevertheless mutual. It has been demonstrated experimentally that the host may thrive without the symbiotic bacteria and that the bacteria occur normally in the soil and that they will readily develop in artificial culture media. This shows conclusively that the symbionts are not absolutely dependant upon each other. Host and parasite, however, thrive much better when in symbiotic association, especially in poor soil.

2. INDIVIDUALISM.

In individualism is reached the acme of mutualistic association. As already explained, the conditions of this occurrence require that one of the symbionts be absolutely dependent upon the mutual relationship. The phenomenon is typically met with in lichens. In these plants we find the nutritive interdependence so marked that a new individual is formed, which in its morphology and physiology is wholly different from any of the symbionts. From the historical review of the Schwendenerian period we learned that in lichens we have an association of a fungus with an alga or algae. It has been demonstrated experimentally that while the algal portion is capable of existing independently, the fungal portion can not do so, that is, the symbionts are not mutually dependent. Individualism will have reached its highest development when all the members of the symbiotic relationship are incapable of existing independently. There is no doubt that in time this will be the case in our present lichens. Since the fungus has lost its power of independent existence as a result of the symbiotic association it is reasonable to assume that the alga likewise is undergoing a change indicative of a more highly developed dependence upon this association. It seems quite evident that it is more difficult to cultivate the lichen-algae than the corresponding free forms.

We shall now very briefly explain the difference between individ-

[1] The student is advised to consult the following works giving a condensed review of the phenomenon of mutualism as it occurs in the Leguminosae:

Frank, A. B. Lehrbuch der Botanik, 1: pp. 255–275. Leipzig. 1892.

Atkinson, G. F. Contribution to the biology of the organisms causing leguminous tubercles. Bot. Gaz. 18: 157, 226, 257. 1893.

Schneider, A. Observations on some American Rhizobia. Bull. Torr. Bot. Club, 19: 205–218. 1892.

ualism, as met with among lichens, and mutualism. These explanatory statements will be more fully discussed in other chapters.

In their development lichens stand alone. They occur in places where neither alga nor fungus could exist independently. Jumelle has proven experimentally that they can resist much greater extremes of heat and cold than other chlorophyll-bearing plants. Every observer of nature is familiar with their wide distribution and wonderful power of adaptability. They are of slow growth and are endowed with an exceedingly long life period. The symbionts unite to form a microcosm which not only performs the life functions originally inherent in both, but also additional life functions which it has acquired during its phylogeny as a lichen. The fungal symbiont, considered by itself, still retains at least a part of its ancestral function of saprophyte; it has acquired in addition the habits of an obligative symbiont upon the enclosed alga. The algal symbiont, whose function is that of assimilating CO_2, must be looked upon as a facultative symbiont, since it can exist and mature independently. As already stated, the fungal symbiont is incapable of maturing into an independent fungus; it is absolutely dependent upon the mutualistic association. Considering the lichen as a unit we find that the fungal portion supplies the symbiotic algae with water containing soluble food substances taken from the substratum; in return the algae supply the fungi with products of assimilation (carbon compounds).

The question bearing directly upon the discussion of individualism is whether lichens shall be considered as autonomous structures or not; that is, shall we consider lichens as modified fungi in agreement with Schwendener and his followers, or shall we consider them as a distinct class in agreement with Reinke? From the very nature of individualism it is evident that the resulting structure is a morphological unit in the full sense of the word. That is, a lichen is neither fungus nor alga, but a new individual which should be given a definite position in the vegetable kingdom. It is an independent individual because we find that on separating the symbionts the individual is destroyed, as has already been indicated. There is, perhaps, no doubt that in the lowest forms of lichens the fungal symbiont may develop to maturity without its algal symbiont, but this is not the case in the higher forms. These probable exceptions to the rule do not disprove that lichens are autonomous, nor do they warrant the method of classification adopted by Schwendener.

3. CONTINGENT MUTUALISM.

Contingent mutualism is a term designating a form of symbiosis which is quite frequently met with among lichens and elsewhere but which has received little attention. Besides the constant symbiotic algae of lichens enclosed by the tissues of the thallus there occur algae which are always found on the outside of the thallus or which, at least, never penetrate the lichen tissue very deeply. Sometimes these algae occur on the upper surface of the thallus, sometimes on the lower surface, sometimes in or among the apothecia. They may be present in one plant, while in another lichen of the same species none may be found. That is, this form of symbiosis is not constant in its occurrence; hence, it is designated as contingent. It has not been ascertained experimentally whether it is in reality a mutualistic, indifferent or antagonistic symbiosis. It certainly does not seem to be antagonistic, because in lichens bearing a large number of these accidental algae we do not find the least indication of any harmful influence; the lichens thus affected seem, indeed, to be uncommonly thrifty, which suggests an additional or secondary mutualism. The fact that this association does not result in any noticeable structural adaptation would seem to be evidence that the elective affinity between the symbionts is only slight. That there is some elective affinity is evident from the fact that one and the same species of algae usually occurs on representatives of certain lichen genera. For example, *Sirosiphon pulvinatus* and a species of *Nostoc* occur on *Umbilicaria* and *Gyrophora; Fleurococcus vulgaris* on *Parmelia* and *Physcia; Pleurococcus punctiformis* on young *Cladonia* and *Baeomyces*. The three algae mentioned are the principal forms which enter into contingent nutritive association with lichens.

Under this form of symbiosis I do not include the occurrence of algae upon dead or decaying lichen-thalli, which is of frequent occurrence and is not a case of symbiosis. Nor do I include the unmistakably mutualistic symbiosis met with in the so-called "pseudolichenes," as *Lepra viridis* and *Amphiloma*.

CHAPTER III.

THE GENERAL MORPHOLOGY AND PHYSIOLOGY OF LICHENS.

INTRODUCTION.

By way of introduction to this branch of our subject it is highly important to call attention to the interrelation of morphology and physiology, which is of special significance in the study of the lower groups of plants, fungi, lichens, and algae in particular. The investigator soon finds that morphological conformations of plants and plant organs coincide with certain functions and, *vice versa*, certain functions coincide with definite morphological characters of plants and parts of plants. It is true that there are a number of scientists who believe that morphology and physiology should be kept separate for didactic purposes; they even go farther and subdivide these main divisions and endeavor to teach each subdivision as a distinct subject.

The anatomical-physiological tendency, which received such a strong impetus through the influence of Schwendener and his pupils, is slowly gaining a footing in England and America. Heretofore it has been customary to devote almost exclusive attention to the morphology of plants; the physiological significance of morphology has been neglected.

In order to avoid any erroneous conclusions as to the meaning of the terms morphology and physiology an outline of their limitations as employed throughout this book is given. Morphology treats of macroscopical (gross anatomy, morphology in the narrower sense) as well as microscopical structure (minute anatomy or histology). Physiology treats of the life phenomena of cells, tissues, organs and individuals. Vegetable pathology (teratology, abnormal physiology) and the corresponding pathological morphology are subordinated to physiology and morphology respectively.

I. ORGANS OF ASSIMILATION.

1. THE THALLUS.

The thallus is the alga-bearing assimilative portion of lichens. This comprehensive definition would also include the thalloid ex-

ciple, which contains algae, and is, therefore, assimilative. The term is, however, usually limited to the alga-bearing portion, exclusive of apothecia. On account of the perfect mutualistic adaptation of the lichen symbionts we find some very marked structural characters to meet the requirements of different cases. In the lower forms of lichens this structural adaptation is not so readily recognizable, but in the higher forms the physiological and mechanical adaptations are, in fact, more marked than they are in the higher plants.

We will now take up the discussion of a typical foliose thallus because in it the morphological differentiations are most highly developed. After having a thorough understanding of the highest type of thallus there will be little difficulty in understanding the lower forms. The following are the tissues met with in a vertical section of the thallus of *Sticta*.

(*a*) *Tegumentary Layer.* (*Dermis.*)
(*b*) *Upper Cortical Layer.*
(*c*) *Algal Layer.* (*Gonidial Layer.*)
(*d*) *Medullary Layer.*
(*e*) *Lower Cortical Layer.*

These layers will be described in this order; the rhizoids, cyphellae, breathing pores, cephalodia and other accessories of the thallus will be treated independently.

(*a*) *The Tegumentary Layer.* (*Dermis.*)

This is the uppermost layer of the thallus and is usually rudimentary or wanting, except in the higher lichens, especially *Sticta* and *Stictina*. It consists of several layers of flattened hyphal cells extending at right angles to the underlying cortical cells. The cells are rather irregular in form; their walls are usually more gelatinous than those of the cortical layer. The walls of the more internal cells are frequently slightly colored, due to a deposit of lichenic acid. The outermost cell-walls are, however, perfectly colorless and gelatinized. Sometimes the outermost cells develop hair-like prolongations whose function is not definitely known. In *Peltigera aphthosa*, for example, they doubtless serve to retain the soredia, which subsequently develop into cephalodia. They, perhaps, also serve to retain moisture. The dermis contains intercellular canals which are continuous with the canals of the cortical layer below. The outermost cells are continually removed by abrasion, while new

ones are formed from the cortical layer. The change from cortical to tegumentary cells consists in a retardation of growth in a vertical direction and a stretching combined with growth in a horizontal direction. As a result of these combined influences the cells become much flattened.

The primary function of the dermis is, doubtless, to prevent the sudden and excessive evaporation of moisture. It also provides a mechanical protection to the underlying tissues.

(*b*) *The Upper Cortical Layer.*

This layer, in different degrees of perfection, is present in all warty, squamose, foliose and fruticose thalli. It is usually designated as a semicortical or semiparenchymatous tissue. Structurally it certainly resembles very closely the parenchymatous tissue of higher plants. The cells are somewhat elongated in a vertical direction and lie in actual contact; in outline they are quite irregular; the walls are usually considerably thickened, especially at the angles; the lumen is in part filled with air. The cells of this layer are directly continuous below with the hyphal cells of the algal layer and above with those of the dermis. There is a continual regeneration or development of new cortical cells proceeding upward from the algal layer, while the upper cortical are converted into dermal.

The cortical layer varies greatly in thickness in different species as well as in different portions of the same thallus. From the fact that the thallus performs the function of assimilation as well as that of mechanical support, it is evident that the structures destined to perform these functions must be suitably adapted and arranged with reference to each other. The upper cortical layer, whose function is primarily mechanical, is variously modified so as to adapt it to the requirements of the underlying assimilating tissue. This is very beautifully shown in *Solorina saccata*; in this species the lower outline of the upper cortical layer is serrate, that is, the cortical layer is alternately thicker and thinner; this gives great mechanical support and at the same time favors the grouping of the algae near the surface for exposure to the influence of sunlight, and to permit the exchange of gases. We find this layer thickest in those lichens having no lower cortical layer, very likely because the exchange of gas can readily take place downward. There are, however, other provisions to permit

the ready exchange of gases; as, for example, the breathing pores and the cyphellae. The breathing pores are the intercellular canals met with in the upper and lower cortical layers, which are continuous with those of the dermis; they are especially numerous in the thinner portions of the layers. The breathing pores, and especially the cyphellae, will be more fully discussed in another chapter.

The primary function of this layer is usually mechanical. Two other functions almost equal in importance are those of protecting the underlying tissues, especially the algae, and preventing the sudden and excessive evaporation of moisture. That the primary function is purely mechanical in most cases, is evident from its structural adaptations in form and position to meet mechanical requirements. In some lichens it is likewise evident that the primary function is not mechanical, since we find special mechanical tissues distinct from the cortical layer, as, for example, in the podetia of *Cladonia* and in some species of *Gyrophora*, as well as in many of the fruticose thalli. In these cases the prime function is evidently to protect the underlying algae.

(*c*) *The Algal Layer.* (*Gonidial Layer.*)

This is by far the most important structure of the thallus. It contains the symbiotic algae whose special function is that of assimilation. The layer consists of hyphal filaments continuous with the cells of the cortical and medullary layers, and the algal cells which are in more or less intimate union with the terminal branches of the hyphae; it varies considerably in thickness; in the same species it is thickest in the young growing plant; in the older portions of the thallus the algae are less numerous. As already indicated, the assimilating algal layer makes suitable concessions as to position to the mechanical tissue. As a rule, the algae are most numerous where the cortical layer is thinnest.

The subject of greatest interest is the relation of the algae to the hyphae. It will be remembered from the historical review that Schwendener, in 1863, and others at one time, believed that the algae (gonidia) develop from terminal branches of the hyphal filaments. From this it is evident that they recognized the close organic union. It is, however, also evident that this association is not very intimate in many forms of lichens, for instance in the Collemaceae, in which the algal symbiont is represented by the genus *Nostoc*. We find the

closest union in lichens whose algal symbiont is represented by *Cystoccocus humicola* Näg; this alga occurs in far the greater number of species.

The forms of union between hyphae and algae are separated into three kinds: 1, Simple contact; 2, Extracellular haustoria; 3, Intracellular haustoria.

1. In this form of association the hyphae and algae are simply contiguous. The hyphae seem to undergo no change in form or development. This is especially the case in those lichens in which *Nostoc* or *Rivularia* occurs (so-called gelatinous lichens). In *Lichina* for instance, the chains of *Rivularia* lie parallel and in contact with the hyphal filaments. I have been unable to detect any influence that the algae may have upon the direction of growth in the hyphae. The same may be said of the Collemaceae. It is, nevertheless, evident from the life histories of the individuals of the groups mentioned, that the symbiotic relationship is very highly developed. From observation it also becomes evident that this contact-association prevails in lichens bearing algae which are naturally enclosed by a gelatinous coat; what influence this coat has on the symbiotic association has not been explained. (*Pl. 1. f. 2.*)

2. In the majority of lichens the algae are enclosed by numerous short terminal branches of the hyphal filament. Whenever a hyphal filament comes in contact with an alga the contact surface is retarded in growth, and, as a result, the filament begins to curve about the alga. The presence of the alga also causes the development of short hyphal branches which wind about the alga in the manner just mentioned. These branches are not only short, but they are usually much thinner and their walls more delicate than the normal branches; they are also much more frequently septate. As the term extracellular haustoria indicates, these enveloping terminal filaments never penetrate the algal cell. The interchange of food substances takes place by osmotic action through the hyphal and algal cell-walls. The haustoria differ greatly in the degree of development. In some instances they are few in number and very loosely united with the algae; when most completely developed they form a network or covering closely united with the alga, so that it is almost impossible to separate the symbionts. (*Pl. 1. f. 3, 4.*)

3. This is, doubtless, the highest form of symbiotic association occurring in lichens. Here we find that the haustoria of the hyphal

filament penetrate the alga; this penetration varies greatly in degree; the tip of the haustorium may pass through the algal cell-wall, forming a somewhat expanded filament between the wall and cell-plasm. In its highest development the haustorium, after entering the algal cell, develops a much-branched network which encloses but does not penetrate the cell-plasm. This haustorial network is made up of delicate gelatinized hyphal branches. Intracellular haustoria are comparatively rare; I have observed them most frequently in young growing species of *Cladonia*, *Parmelia* and *Stereocaulon*. The question as to the manner in which the haustoria gain entrance into the interior of the alga requires further study; also the question of the biologic significance of this form of union. Can the liberated algal cell with its haustoria develop into a new lichen? It consists of both symbionts, all that is required for the formation of a new thallus; it may, however, be that the haustorium when separated from the parent filament can no longer continue to grow. Algae which have intracellular haustoria have also, as a rule, extracellular haustoria. The plasmic contents of the algal cell are in time entirely absorbed by the haustorium, so that nothing remains but the algal wall enclosing the hyphal network. (*Pl. 1. f. 5, 6.*)

(*d*) *The Medullary Layer.*

In the majority of lichens this layer is much thicker than any of the others; it usually consists almost entirely of hyphae; rarely we find distributed through it small groups of algae. The hyphal filaments consist of branching much elongated cells and are morphologically closely allied to ordinary fungal hyphae. The cell-walls do not become gelatinized like those of the cortical and dermal layers, and, like all lichen tissues, do not stain readily. Occasionally we find a coloring matter deposited within or upon the cell-walls; as a rule, however, they are colorless. In the middle portion of the layer the hyphae extend in a direction parallel to the main axis of growth: above and below they extend vertically to the cortical layers with which they are continuous.

Structurally the medullary layer forms a marked contrast to the cortical layers. It consists of a network of very loosely interwoven hyphae with large air spaces. In this respect it is analogous to the spongy tissue of the foliage leaves of higher plants. Occasion-

ally we find groups of tissue elements distributed through this layer whose primary function is mechanical. This is, however, rare; mechanical tissues as a rule occurring outside of the medullary layer.

In some lichens, especially the so-called Lichenes gelatinosi (Collemaceae), there is no distinct medullary layer; that is the algal and medullary layers are, so to speak, intermingled. There is no medullary tissue proper in the crustaceous lichens, since none is necessary at least as far as the requirements of aeration are concerned.

Structurally this layer is adapted to perform two functions. The hyphae conduct food substances such as water, mineral salts, carbon compounds, nitrogen, hydrogen, to and from the algae. They form the paths of exchange between the products of assimilation formed by the algae and the soluble food substances taken up by the fungal portion. Much work is, however, yet to be done in the physiological study of these functions.

According to Zukal (110) the medullary hyphae also serve as storage tissues, accumulating for future use various carbo-hydrates (lichenin, isolichenin), gelatine, fats and fatty oils. Lichenin is stored in the cell-walls, causing them to become considerably thickened. The excess may or may not become reabsorbed in the future life processes of the plant. Fat is stored within the cells and varies considerably in amount but never occurs in large quantities; it seems probable that the fat is stored at one point to be again utilized at some other point in the same plant. Fat also frequently occurs in the spores, where it doubtless plays an important part in the processes of germination. The sphaeroid-cells occurring in the calcivorous crustaceous lichens are special fat-storing structures. It is as yet a disputed question whether this fat is waste product or whether it is really utilized in further metabolic processes.

(*c*) *The Lower Cortical Layer.*

Structurally this layer very closely resembles the upper cortical layer. The cells have the same essential characters. They are somewhat elongated in a direction vertical to the thallus. As a whole this layer is thinner and the cells are more loosely united than the corresponding cells of the upper cortical layer. The dermal layer is always wanting. Quite generally there occurs a dark coloring substance in the cell-walls. This layer is wholly wanting in

many of the higher foliaceous lichens, as, for example, in *Nephroma*, *Psora* and *Peltigera*.

From the lower surface are developed the rhizoids. In it also occur the cyphellae, whose structure and function will be considered later.

The principal function of this layer is doubtless mechanical. Since it is continuous below with the rhizoids and above with the medullary hyphae, it is evident that the cortical cells must transmit the soluble food substance taken up by the rhizoids. This layer is more highly hygroscopic than the upper cortical.

The student of comparative morphology will be impressed with the close analogy between a typical foliose thallus and a foliage leaf. This analogy is close both as to structure and function. Morphologically we find the following similarities: The epidermal layers (upper and lower) of the leaf may be compared to the upper and lower cortical layers (inclusive of the dermis) of the thallus; the palisade layer to the algal layer; the spongy tissue to the medullary layer; the vascular bundles (veins and midrib) to the hyphal bundles (mechanical tissue). The special function of the tissues in the leaf is also closely similar to the special function of the corresponding tissues in the thallus; that is, epidermis (of leaf) and cortical layers (of thallus) have a mechanical and protective function; palisade cells and algal layer are assimilative; spongy tissue and medullary layer form the aerating and conducting tissue; the vascular bundles and hyphal bundles are essentially conducting and mechanical.

2. TYPES OF THALLI.

There are three types or forms of lichen-thalli recognized by nearly all lichenologists: (*a*) The crustaceous; (*b*) The foliose (foliaceous, frondose); (*c*) The fruticose (fruticulose). It must not, however, be supposed that these types are absolutely distinct; there are all intermediate forms between the simplest network of hyphae intermingled with a few algae and the most highly developed fruticose thallus. Since the great advance made in the morphological investigations of lichens it becomes doubly necessary to draw some lines of distinction between these different forms of thalli. A recognition of these characteristic forms is important from the standpoint of morphology and physiology as well as in classification. As taxo-

nomic characters they are of importance only in the minor subdivisions. The attempt to classify all lichens under the great divisions crustaceous, foliose and fruticose is wholly artificial and must be discarded for a more scientific method.

(*a*) *The Crustaceous Type.*

As is to be expected from the origin and development of lichens, this thallus occurs only in the lower forms—those which have not yet reached any high degree of development in the scale of lichen evolution. The cortical tissue is typically wanting; in its simplest form, as met with in the lower Caliciaceae, and in all hypophloeodal thalli, there is merely a hyphal network bearing groups of algae which as a rule are quite uniformly distributed, so that there is scarcely any distinction into hyphal and algal layers. It is a dorsiventral structure, although not well marked. The lower surface is distinguished from the upper by the presence of numerous hyphae which serve the function of rhizoids.

In the more highly developed crustaceous thalli three layers may be recognized: 1. The upper, usually a colorless hyphal network devoid of living algae but containing in its meshes the cell walls of dead algae, which intermingled with the hyphae aid in forming a rudimentary protective covering for the underlying algal layer; the hyphae of this layer are more branched and the cell walls somewhat more thickened and gelatinized than in the normal hyphae; they also have a tendency to extend in a vertical direction. 2. The layer immediately beneath the foregoing consists of the algae enclosed by the hyphae or united with them. On making a comparative study of this layer and the algal layer of higher lichens we note the following differences: The algae are in much less intimate association with the fungal hyphae; the haustoria are less numerous and less perfectly developed and rarely penetrate the algal cells; the uppermost algae continually die, while new ones are formed by direct division. 3. Below the algal layer is another layer of hyphal tissue free from algae. It differs from the upper hyphal layer in that the filaments are somewhat less branched, and they usually extend in a longitudinal direction; the cell-walls are also thinner and less gelatinized. It corresponds to the medullary layer of the higher lichens. Below this layer are the hyphae, which perform the function of rhizoids and which usually extend in a vertical direc-

tion into the substratum. The oil-bearing cells of calcivorous crustaceous lichens occur among the rhizoidal hyphae.

Many of the crustaceous thalli develop below the surface of the substratum. If below a rock surface they are said to be hypolithic; if below the surface of the bark they are said to be hypophloeodal. Here also it must be remembered that there are all intermediate forms between completely hypolithic and epilithic and between completely hypophloeodal and epiphloeodal thalli.

(*b*) *The Foliose Type.*

In general it may be stated that under the foliose (foliaceous, frondose) type are included all expanded distinctly dorsiventral thalli having at least an upper cortical layer. This definition includes warty, isidioid and squamose thalli. In *Collema*, however, we find an exception. Here we have a very marked thalloid expansion but no cortical layers.

It must be borne in mind that there is a great difference in the morphological characters of the cortical tissue. It may be highly developed, or so deficient as to be scarcely recognizable. In the lower lichens it usually consists of a thin layer of parallel or irregularly interwoven agglutinate hyphae. In this structure the cells are readily separated by various alkaline solvents. The cells are comparatively long with gelatinous cell-walls (Lichen cellulose, lichenin). In the more highly developed foliose thalli the cortical tissue consists of short cells with large cell lumina. The walls of the adjacent cells are very closely united; strong alkalies dissolve the membranes with difficulty. There are all gradations between this form and the most rudimentary structure. It has been found impracticable to recognize distinct forms of cortical tissues as some authors have done (Zukal). By cortical tissue is, therefore, here meant a hyphal structure of closely agglutinate cells with few intercellular spaces.

The foliose thallus is very variable in size; it may be so small as to require a lens for its detection, as in *Dermatocarpon* and in warty thalli. It reaches its maximum development in *Gyrophora* and *Umbilicaria*, which may be a foot in diameter or more. It may be entire or variously lobed and divided; the lobes may be rounded, oblong or strap-shaped. As a rule, it is held to the substratum by means of the rhizoids. There are, however, also special mechanical struc-

tures to resist the lateral tearing and lifting force of air currents (see discussion of mechanical adaptations).

Foliose thalli are, as a rule, typically dorsiventral in structure. The upper portion, turned toward the sunlight, is primarily adapted to perform the function of assimilation; the lower portion is adapted to conduct food substances. There are also remarkable relative adaptations of mechanical support and physiological function. The anatomy of the foliose thallus has been explained in the discussion of the thallus.

(*c*) *The Fruticose Type.*

As the type of the fruticose thallus I have selected *Usnea barbata* in which it attains its highest development. In structure it is perfectly radial. There are, however, all gradations between a typically foliose and typically fruticose thallus. For convenience of classification I have included under fruticose all vertical ascending or pendant, structurally centric, thalli having flattened or cylindrical branches and which are attached at one point (umbilicus). They may be sparingly branched, as in *Pilophoron*, or much branched, as in *Stereocaulon* and *Usnea*. As already indicated, there may be marked tendency toward dorsiventrality, as in *Cetraria* and *Ramalina;* it is less marked in *Evernia*. Typically radial structures are met with in *Pilophoron*, *Stereocaulon*, *Bryopogon*, *Alectoria*, podetia of *Cladonia*, etc. The general histological characters of this thallus are similar to those met with in the foliose type; hence we shall content ourselves with a description of the arrangement of tissues and a hasty comparison of homologous tissue elements.

There is no tissue deserving the name of epidermis. The outer cylindrical layer which corresponds to the cortical layer of the foliose thallus is not typically cortical in structure. The hyphae usually extend at right angles to the longitudinal axis; sometimes they extend longitudinally. The cells are longer, the cell-walls much thicker and more gelatinized, the cell lumina more deficient than in the foliose cortex. Branching of the hyphae does not frequently occur. Gelatinization of the cell walls sometimes proceeds to such a degree that scarcely any structure can be discerned; this is especially true in those cases where the hyphae extend at right angles to the longitudinal axis and are considerably branched. If the hyphae extend longitudinally, as in *Theloschistes* and *Ramalina*, there is less

difficulty in tracing the outlines of the cells, provided the sections are sufficiently thin. Sometimes this cortical layer is not continuous; that is, it occurs in patches corresponding to the patches of algae beneath. There is no doubt that the prime function of this layer is protective and preventive of excessive evaporation of moisture.

Immediately following the cortical layer is the algal layer which is quite generally more deficient than the correspondiug layer in the foliose thallus. The association of the algae and hyphae is similar to that described in the foliose type. As indicated above, this layer is not always continuous. In the less highly developed fruticose thalli, as *Pilophoron*, the algal layer occurs in patches corresponding to the superimposed cortical areas. The medullary layer is usually deficient, except in *Alectoria* and *Bryopogon*, where it fills the entire central cavity as a very sparingly branched network of hyphae. Structurally it is not different from the medullary layer of foliose thalli.

In the majority of fruticose thalli the medullary layer is followed by a mechanical and conducting tissue of longitudinal hyphae. This tissue may form either a hollow cylinder, as in the podetia of *Cladonia*, or a solid strand, as in *Usnea*. The cells are much elongated, very sparingly branched, and extend parallel to the longitudinal axis of growth. The cell-walls of this tissue are much less gelatinized than those of the cortical cells.

In fruticose thalli built on the plan of a hollow cylinder, we find numerous transverse supporting tissues, consisting of bundles of hyphae. Their special function is mechanical; that is, they prevent the collapse of the cylinder due to sudden changes in turgor as well as to lateral pressure.

The question whether the fruticose or foliose thallus is the more highly differentiated is rather difficult to decide. From a purely structural point of view it would seem that the fruticose thallus is the higher. There are several well-marked differences between the foliose and fruticose types. The most important is the predominance of structural adaptations favoring the assimilative function in foliose thalli, while the mechanical adaptations predominate in fruticose thalli. There is little doubt that the fruticose thallus has been phylogenetically derived from the higher crustaceous forms; perhaps, in some cases, from some of the lower foliose forms. The differences here indicated will be more fully explained in subsequent chapters.

3. BREATHING PORES.

There are various structural adaptations met with among lichens, whose special function is that of aeration, that is, of facilitating the exchange of gases resulting from the processes of assimilation. Some of these adaptations are readily visible to the naked eye, such as the pores in some of the Cladonias and other fruticose lichens, also the inflated thalli of some Parmelias. We have already shown that the outer cortical layer of the lower fruticose lichens is frequently incomplete, thus making it possible for the assimilating algae to come in contact with the necessary CO_2 of the atmosphere. The absence of the lower cortical layer in many foliose lichens permits the entrance of air. It is evident that thalli with both upper and lower cortical layers must have special structural adaptations to facilitate the exchange of gases; these we shall now briefly discuss.

On careful examination of a thin vertical section of a foliose thallus it is found that the cortical layers are not continuous. The upper cortical layer, especially, contains intercellular canals or pores, which open above to the exterior and below into the algal and medullary tissues. These canals are especially numerous in the thin areas of the upper cortical layer; they are considerably branched and pass upward or outward until they arrive at the epidermal layer, where they assume a horizontal course, because the cells of this tissue are elongated horizontally. In the dry state the cell-walls of the cortical cells become shrunken, allowing the angles to come in contact, thus closing the pores and reducing the loss of moisture to a minimum. With the increase of moisture the cell-walls become swollen and the intercellular canals enlarged, thus enabling the assimilation of CO_2 to take place. These canals, which are designated breathing pores, occur in *Nephromium*, *Solorina*, *Parmelia* and other genera. They occur even in the upper cortical layer when no lower cortical tissue is present. As a rule, however, they are wanting in foliose lichens with only one cortical layer. Again they may occur in both upper and lower cortical layers. In *Sticta* and *Stictina* they predominate in the lower cortical layer. Their relation to the cyphellae will be explained in the discussion of these organs.

4. CYPHELLAE.

The structures known as cyphellae have long been familiar to lichenologists. Haller (1776) was the first author who called atten-

tion to them. He described them as "white circular depressions," which was about all that was known concerning these structures at the time. Acharius was the first to introduce the term cyphellae. In spite of the fact that these formations have been observed for more than one hundred and twenty years, little is known of their origin and development, and still less of their function.

The cyphellae occur almost exclusively in the genera *Sticta* and *Stictina*; in position they are limited to the lower surface of the thallus. Structurally they are circular breaks in the lower cortical layer, filled in by a secondary tissue formation. They begin their development above a breathing pore in the lower cortical layer. That is, the pore, which is simply an intercellular canal, is first formed and becomes enlarged by the separation of the cells. While this pore is yet very minute, the secondary tissue or cortex begins to develop in its immediate vicinity. The hyphae of the medullary layer give off a number of nearly spherical or short branches which close the enlarging pore-opening; the formation of the secondary cortical tissue keeps pace with the enlargement of the opening in the primary cortical tissue.

As to structure, two forms of cyphellae may be recognized. Form 1 is seen in *Stictina damaecornis*. The cyphellae appear as circular depressions, concave inward, the edge of the primary cortex forming a constricted outer margin, which projects somewhat beyond the surface of the cortical layer. The cells of the secondary cortical formation are nearly spherical, loosely united, leaving numerous intercellular spaces; they extend in a direction at right angles to the outer surface. In thickness this scarcely equals the primary cortex. Its outer surface is usually smooth, devoid of rhizoids and paler in color than the primary cortex. The cell-walls are quite thin, usually more so than those of the medullary cells. (*Pl. 2. f. 1.*)

Form 2 occurs in the majority of *Stictas* and *Stictinas*. It differs from the former in several respects. The secondary tissue consists of a dense network of short branching hyphae whose longitudinal axes extend at right angles to the surface of the cyphella. Instead of a depression, as in the former case, there is usually a protrusion of the secondary tissue. The margin of the primary coxtex also projects somewhat, but its outline is less regularly circular. (*Pl. 2. f. 1.*)

Both forms of cyphellae are sufficiently large to be seen by the naked eye. They are distributed over the convex areas of the lower surface of the thallus; none ever occur in the grooves. As already explained, they begin their development near the tip of the growing thallus, reaching their mature size at a distance of a few millimeters from the margin. In thalli whose lower surface is nearly flat, they are quite uniformly distributed.

Acharius applied the term cyphellae to the form first described; the second form he believed to be soredia. Nylander retained the name cyphellae for the first form; the second he designated as pseudocyphellae. There is no morphological or physiological reason why the latter should be designated as "false." Indeed, it would be more consistent to designate the former as false, since they are of less frequent occurrence. Stitzenberger (1895) retains Nylander's distinction as to true and false cyphellae and further subdivides them as to color into white and yellow. This author also considers these structures of great importance in his classification of the Stictei.

Having thus briefly treated the morphology of the cyphellae we will refer to their probable physiological significance. As already indicated, some of the older lichenologists looked upon them as vegetative organs of propagation, similar to the soredia. They are not soredia, since they usually contain no algae. That the second form may accidentally contain a few algae in its meshes, is possible, as we find occasional groups of algae distributed throughout the entire medullary layer. It is, however, unreasonable to suppose that they normally contain algae, since their position is not suitable for the ready development of these symbionts. There are several reasons which make it seem probable that the cyphellae have to do with the function of aeration. As already indicated, the breathing pores are analogous in function to the stomata of higher plants; from the relation of the cyphella to the breathing pores it is quite reasonable to assume that their function is to admit air into the interior of the thallus; in their mode of development and in position they are analogous to lenticels. It is also found that the upper cortical layer of *Sticta* and *Stictina* is usually without breathing pores, which is accounted for by the fact that the lower cortical layer contains the necessary pores and openings for the admission of air.

5. THE CEPHALODIA.

Various outgrowths from the lichen-thallus had been observed by several authors previous to Acharius. These outgrowths included true cephalodia as well as secondary thalloid formations and were variously designated as corpuscula, maculæ, etc. Acharius (1803) first proposed the term cephalodium and rightly applied it (in the sense of Forssell) in the lichen-species *Peltigera aphthosa*. Flörke (1819) designated them sponge-like outgrowths (corpuscula fungosa) and gave a fairly accurate description of them as they occur in *Stereocaulon* and *Pilophorus robustus*. Wallroth describes them under the name phymata and emphasizes the fact that they differ in structure as well as in color from the normal thallus; he classified them as to form. Fries (1857) described their external appearance quite accurately, but did not understand their true nature and origin; he believed that the gonidia of the cephalodia were subject to variation in color and form. Nylander considered the cephalodia as pathological or parasitic structures, and pointed out the difference between the normal gonidia of the thallus and the gonidia of the cephalodia. Schwendener, Bornet, Babikof and others studied these structures without making, however, any important additions to the work done by Nylander and Fries. Winter (1877) gave us the first more accurate descriptions of the cephalodia as they occur in *Sticta* and *Solorina*. Minks (1879) describes the cephalodia as "gonotrophies" and expresses the opinion that they are of wide occurrence; he states that they are constantly present in *Lecanora gelida*, *Stereocaulon ramulosum* and *Peltigera aphthosa*. Branching cephalodia occur regularly upon *Sticta amplissima* found in Europe, while they are regularly absent in our American species (Forssell). By far the most complete and important discussion of this subject is that by Forssell. This author made a careful study of their origin, development and distribution. The student is referred to his original communication as it appears in Flora for 1884; his classification is as follows:

I. *Cephalodia vera* (organically connected with the normal lichen structure).

A. *Ceph. epigena* (*perigena*) (occuring upon the upper surface of the thallus).

1. *Ceph. tuberculosa* (Peltidea aphthosa).
2. " *lobulata* (Sphaerophorus stereocauloides).
3. " *clavata* (Stereocaulon ramulosum).

B. *Ceph. hypogena* (occurring upon the lower surface of the thallus).

1. *Ceph. thalloidea* (Peltidea venosa).
2. *Ceph. immersa* (Nephroma and Lobaria).
3. " *placodioidea* (Lecanora gelida).
4. " *granuliformia* (Lecidea panaeola).
5. " *fruticulosa* (Sticta amplissima).

II. *Pseudo-cephalodia* (apparently not organically united with the lichen structure).

As to the algal types occurring in the various cephalodia the following groups are represented, according to Forssell:

1. Nostocaceae.
2. Stigonemaceae (Sirosiphon).
3. Scytonemaceae.
4. Chroococcaceae.
5. Oscillariaceae.

It is quite evident that this author has included under pseudo-cepholodia many of the occurrences which I have included under contingent symbiosis. It is also probable that some of his cephalodia vera have no organic connection with the lichen structure and are more likely to be forms of contingent symbiosis. Inasmuch as many of the cephaloid structures are not sufficiently understood, I will now give a more detailed description of undoubted cephalodia; these may readily be divided into two kinds, endotrophic and ectotrophic.

(*a*) *Ectotrophic Cephalodia.*

In general a cephalodium may be defined as an abnormal development within or upon the lichen thallus induced by some foreign alga. An ectotrophic cephalodium is one which occurs upon the thallus. The form which has been more particularly studied occurs regularly on *Peltigera aphthosa* (L.) Hoffm. In this species the cephalodia occur as small granular or warty elevations upon the upper surface of the thallus; they are especially numerous toward the margin; they vary in size from very small, nearest the margin, to about the size and form of a pin head toward the center of the thallus.

These cephalodia originate near the apex of the thallus. As far as it has been possible to observe, they result from the development of soredia (of some *Rivularia*-bearing lichen) which are carried to the thallus, where they are retained by the short hyphal branches which

extend above the surface of the upper cortical layer (Plate 3, fig. 1). This cephalodium is, therefore, a small thallus of some other lichen and has no organic connection with the plant upon which it occurs. Soon after the soredium locates upon the thallus it begins to grow; the projecting hyphal branches of the cortical layer to which the soredium becomes attached branch and grow in length something after the manner of the algal haustoria. The cephalodium enlarges in all directions, but more horizontally than vertically, which causes it to become flattened; the outer cells soon become cortical; this cortical tissue increases more rapidly at the upper surface, where cortical projections are also formed downward for the purpose of increasing the mechanical support. The cell-walls of the outermost cortical cells both above and below are colored a dark brown; they are otherwise much like the cortical cells of the thallus. The medullary hyphae and the algae fill the entire interior. The algae are arranged in chains which extend in a vertical direction; they are somewhat more closely crowded toward the upper surface.

The presence of this cephalodium has considerable influence upon the underlying structures of the lichen-thallus. The cells of the cortical layer of the latter become elongated and less cortical in structure until in the mature cephalodium the cortical tissue has become medullary. The algae of the thallus immediately below the central point of the cephalodium begin to disappear quite early in the development of this structure. The disappearance of the algae and the cortical tissue keeps pace with the growth of the cephalodium, so that the horizontal diameter of the cephalodium is always a little greater than the diameter of the area devoid of cortex, and still a little larger than the area devoid of algae. The physiological explanation of this structural change in the thallus coincident with the development of the cephalodium is a transfer of the function of assimilation from the areas of the thallus covered by the cephalodia to the cephalodia themselves. The haustorial hyphae of the thallus adherent to the cephalodium and continuous below with the medullary hyphae carry the food substances to and from the cephalodium. Figures 1, 2 and 3, Plate 3, will aid in explaining the development of this form of cephalodium and its relation to the thallus.

As Forssell has shown, there are various forms of ectotrophic cephalodia. The one above described is the most common and typical. Another form is commonly met with among the various

species of *Stereocaulon;* these are very irregular in size and form, though they never become large; the symbiotic algae belong to the genus *Sirosiphon;* in these forms I was unable to determine whether they were organically connected with the lichen-thalli, or whether they are simply small undeveloped specimens of *Ephebe pubescens* living in mutualistic relationship with the *Stereocaulon*-thallus. It is evident that further careful work must be done in regard to the morphology and physiology of cephalodia in order to determine their true nature.

(*b*) *Endotrophic Cephalodia.*

These cephalodia, as the name indicates, occur wholly within the tissues of the lichen-thallus; in this country they are typically developed in *Sticta Oregana* and I have studied them more particularly in that species; they belong to the *cephalodia vera* of Forssell, who has also given a very accurate description of the development and morphology of this form. In the endotrophic cephalodia as they occur in *S. Oregana* the infecting alga is likewise some species of *Rivularia;* they differ structurally from the cephalodia of *Peltigera aphthosa* in that the infecting algae are enclosed by the hyphal tissue of the lichen in which they occur.

The mature cephalodia appear as spherical projections either above or below the thallus, varying in size from a pin-head to a pea. They seem to project downward about as frequently as they do upward, and may occur in any part of the thallus except near the margin. As far as I have been able to observe, they begin their development in the medullary layer of the thallus; I am unable to state in what manner the algae gain entrance to this layer, nor has the mode of infection been accurately observed by any one. The fact remains that when the algae have gained access to the interior they begin to divide, increasing in number quite rapidly, and by a mutualistic effect upon the surrounding hyphae these also undergo more active development. As to the initiative which determines the formation of an inferior or superior cephalodium I am unable to give any satisfactory explanation; it may depend upon a difference of resistance offered by the two surfaces: that is, if development begins nearest the lower cortical layer it will project downward, if nearer the upper cortical layer it will project upward. Both forms are structurally much alike. In the superior form the upper cortical

layer bulges upward more and more, which necessitates increased cell-formation in the layer in order to avoid any breaks in the continuity of the tissue; the algal as well as the medullary layers also curve upward, but the algae decrease in number with the increase in the curvature. In the fully developed superior cephalodium there are only a few algae near the apex, or none; from that point they gradually increase in number until they reach their normal quantity at the level of the algal layer of the normal thallus. Between the algal layer of the thallus and the tissue of the cephalodium proper there is a hyphal tissue devoid of algae, which corresponds in part to the medullary tissue of the thallus. The remaining structure consists of the enormously developed inferior medullary portion of the thallus bearing the foreign algae, which are collected in groups separated by bundles or plates of longitudinal hyphae extending parallel with the algal chains; these bundles and plates no doubt serve a mechanical function.

The inferior cephalodium corresponds to the superior in development and general structure; the algal layer of the thallus, however, remains unchanged; the foreign algae are somewhat less numerous, while there is an increase in hyphal tissue.

Figures 3 and 4, Plate 4, represent the structure of both the inferior and superior cephalodia; the sections were made from young undeveloped tubercles. The full grown forms are represented in the diagramatic figure, 2. Figure 1, Plate 4, is a semidiagramatic vertical section of a young cephalodium before it can be determined whether it will become superior or inferior.

6. THE RHIZOIDS.

The rhizoids are the root-like structures extending from the lower surface of the thallus and penetrating the substratum; they are in all cases hyphal cells more or less modified and continuous above with the hyphal cells of the thallus. Structurally we may divide all rhizoids into three kinds: 1. Those occurring in crustaceous lichens and consisting of a hyphal network of only slightly specialized cells. 2. Those consisting of much elongated simple or slightly branched hyphae with cell-walls firm and considerably thickened; they occur typically in the genus *Mallotium*. 3. This is the highest form and consists of simple or branched bundles of elongated closely adnate hyphal cells whose walls are also considerably thickened and

hardened; these occur in the majority of the higher foliose and fruticose lichens.

1. In the lower crustaceous lichens the rhizoids are not distinguishable in structure from the hyphae of the thallus proper. They form a network of branching filaments whose predominating direction is downward into the substratum; in the case of bark-lichens this network surrounds the cork cells. Lindau and others have proved conclusively that the hyphae never penetrate the intact cells of the vegetable substratum. Among the hypophloeodal lichens there are no rhizoids structurally recognizable as such. Since the thallus is entirely enclosed by the substratum all the hyphae can assist in absorbing soluble food substances; the necessary mechanical support and protection is given by the tissue of the substratum, so that the entire hyphal network is devoted to the absorption and carrying of food substances, which is the prime function of rhizoids among the crustaceous lichens. In the lower lichens saprophytism still predominates, indicating a close functional relation to fungi.

Structurally the rhizoids of crustaceous rock-lichens are very much like those of crustaceous bark-lichens. A prevailing mistaken notion is that the rhizoids *penetrate* the solid rock; this is mechanically impossible; the rock particles nearest the surface are, however, disintegrated by acid secretions from the rhizoids, whereupon the hyphae are enabled to enter the openings and crevices thus formed and enclose the loose insoluble rock particles; the whole is held together by the gelatinized cell-walls of the rhizoids. In this manner the rhizoids may "penetrate" the rock to a considerable depth; in fact, some lichens are entirely imbedded in the loose rock material. The rhizoids of calcareous rock-lichens contain the oil-cells which have been mentioned already.

2. In some of the typically foliose thalli we find very long rhizoids, consisting of single unbranched or sparingly branched hyphal threads (*Mallotium*). The cell-walls are quite firm and considerably thickened; the walls also contain a coloring substance, usually dark. Since these rhizoids are frequently aerial, that is having no connection with the substratum, it is reasonable to suppose that they serve to retain moisture; they are also supposed to protect the plant against the attacks of animals, especially snails (Zukal); in other respects the resemble the forms described in the following paragraph.

3. In the majority of the higher foliose and fruticose lichens the rhizoids are no longer primarily adapted to perform the function of absorption, as is evident from their structure. They do not consist of a network or threads of hyphal branches, but occur in bundles of elongated closely adnate hyphal cells, thus forming also a mechanical tissue specially adapted to resist longitudinal pulling tensions. That this mechanical function is highly important in the larger foliose and fruticose thalli is very evident, but the function of absorbing and conducting food substances is likewise important; it is difficult to determine in many instances which function is the more important. Sometimes the rhizoidal bundles are simple, as in many *Parmelias* and *Physcias*; frequently they are branched, as in the umbilicus of *Umbilicaria* and other genera and in the rhizoids of *Gyrophora* and some *Parmelias*. The so-called umbilicus is a very much enlarged branching rhizoid; macroscopically it has a typical root-like appearance.

Sometimes these rhizoids are likewise aerial and serve to retain moisture as well as to form a suitable nidus for the growth of certain algae (see Contingent Symbiosis). In nearly all cases the rhizoids are colored differently from the thallus, usually black; as to the purpose of this coloring substance, which is deposited in the cell-walls, there is no satisfactory explanation given; it may be possible that it has some influence upon sunlight and the absorption of warmth. According to Zukal the coloring matter in the rhizoids, and elsewhere, forms a protection against the attacks of animals (snails) on account of its disagreeable bitter and acrid nature, due to the presence of lichen-acids; according to the same authority the aerial rhizoids also serve to keep away crawling animals.

7. THE CILIA.

Cilia are slender, rhizoid-like structures which normally occur along the margin of foliose and flattened fruticose thalli; morphologically they resemble the more highly developed rhizoids, from which they are, no doubt, phylogenetically derived. They consist of bundles of hyphal cells, either simple or branched, and are usually black or dark-brown, due to a coloring substance deposited in the cell-walls; some are ash gray, as in those of *Physcia stellaris*. Structurally they are almost identical with the rhizoids; they are, in fact, modified marginal rhizoids, which have assumed an entirely

new function; their cell-walls are quite thick, and contain a high percentage of lichen-acids, which prevent their being eaten by visiting insects or snails. Like the rhizoids, the cilia are highly hygroscopic, and absorb moisture with great avidity; this can readily be observed by bringing a drop of some colored liquid in contact with their tips. It seems evident that the prime function of the cilia is to retain and absorb drops of water; a second and less important function is that of preventing crawling animals from passing to the upper surface of the thallus (Zukal).

III. REPRODUCTIVE AND PROPAGATIVE ORGANS.

1. THE APOTHECIA.

The apothecia are the spore-bearing organs of lichens developed from the fungal symbiont, although the algae enter into their formation in the higher lichens (thalloid exciple); structurally, and in their mode of development, they are closely related to the apothecia of the *Ascomycetes;* their great variability in form and size will be more fully discussed in the descriptions of families and genera. The great majority of apothecia occur on the upper surface of the thallus, either sessile or immersed; in *Nephroma*, however, they occur on the lower surface. Special morphological adaptations occcurring in the apothecia, either for mechanical or protective purposes, will be more fully discussed in another chapter. As in the treatment of the thallus, we shall limit ourselves to the discussion of the general morphology and physiology of the typically developed apothecium, as it occurs in *Sticta*, *Parmelia* and other higher foliose lichens.

(*a*) *The Epithecium.*

The old definition of epithecium is morphologically indefinite; as defined by Leighton and Nylander it is the colored disk of the apothecium; this colored disk, however, includes the upper parts of the paraphyses as well as the remnants of the thallus which were above the disk as the apothecium pushed its way through the upper cortical layer; it is, therefore, evident that the term epithecium includes two morphologically distinct tissues. I have decided to designate only the remnant of the thallus as the epithecium proper; in the majority of mature apothecia this is scarcely recognizable; it consists of the broken down and gelatinized granular remnants of the

cortical cells; it has the same color as the upper ends of the paraphyses.

In the early period of the development of the apothecium this layer, no doubt, plays an important part as a protective covering; whether it is of any use or not in the mature apothecia is not known; it is probable that the coloring substance has some influence upon sunlight in its effects upon the maturation of the spores; it may also serve a protective function similar to the coloring substances deposited in the thallus.

(*b*) *The Thecium.*

This layer occurs immediately below the epithecium and is the most important tissue of the apothecium, because it contains the spore-bearing thekes (spore-sacs, thecae). It consists of the paraphyses and spore-sacs, both of which arise from the hyphae of the hypothecium. The spore-sacs, according to some authorities, arise from a specialized hyphal tissue known as the ascogenous hyphae. In their early period of development it is possible to distinguish these hyphae from the hyphae which produce the paraphyses; they are larger, more irregular in thickness, and the cell-walls are more gelatinized; tincture of iodine usually stains them blue, although this reaction is by no means constant, and in the mature apothecium this difference in structure and in chemical reaction cannot usually be observed. The spore-sacs are the enlarged terminal cells of the ascogenous hyphae which push their way between the paraphyses. At maturity the sporogenous cell undergoes considerable chemical change, especially in the upper and outer portion. In the Caliciaceae the upper portion of the cell-wall is entirely gelatinized, even before the spores have become mature. In the majority of cases only the outer part of the membrane becomes gelatinized; this gelatinous portion readily absorbs moisture, causing the spore-sac to enlarge and to aid in the expulsion of the spores.

The mature spore-sacs vary greatly in the different lichen-groups; as a rule, they are somewhat shorter than the paraphyses and somewhat more expanded above than below; in general outline they may vary from long-cylindrical to nearly spherical. In position they are placed vertical to the hypothecium and parallel to the paraphyses.

The paraphyses are slender hyphal filaments usually colored at the upper ends; they are generally simple; they may, however, be

sparingly or frequently branched; their upper ends, besides being variously colored, are also more or less enlarged. Sometimes they are partially or almost entirely gelatinized, as in the Verrucariaceae. Again, they may be granular, so as to make it difficult to determine their structure. As a rule, they are few-celled, scarcely ever single-celled. They are usually looked upon as as sterile spore-sacs.

The mature paraphyses likewise vary greatly in length, less in thickness; in some cases only the tips are colored, and again the entire thecium is more or less tinged with the coloring substance deposited in the cell-walls. In some lichens the paraphyses unite to form semicortical vertical plates extending through the thecium. Their function is, no doubt, mechanical, and has to do with the ejection of spores.

(*c*) *The Hypothecium.*

The hypothecium is the hyphal structure found immediately below the thecium. In the higher foliose lichens it usually consists of two layers: an upper one, in which the cells extend in a horizontal direction, and a lower one, in which the cells extend in a vertical direction; frequently the two layers can not be distinguished. The cellular structure of the hypothecium varies greatly; in some lichens (especially the higher foliose forms) it is cortical; again there is no trace of a cortical structure, particularly in the lower forms. The cortical tissue of the hypothecium differs, however, from the cortical tissue of the thallus; the cells are smaller and usually more gelatinized. In the non-cortical hypothecium the hyphal cells are rather short and also considerably gelatinized; they are always smaller in diameter than the medullary hyphae.

The margin of the hypothecium forms a part of the exciple, as will be explained more fully later. Here the hyphal threads describe trajectory curves corresponding to the direction of growth; those above the median plane of growth curve upward and enter into the formation of the upper hypothecial layer as well as into that of the paraphyses and spore-sacs; those below the median plane extend downward and enter into the formation of the lower hypothecial layer and the exciple.

In the lower lichens the hypothecium is often colored, usually black, and varies greatly in consistency; sometimes it is quite soft, again it is hard and brittle; it also varies considerably in thickness.

As regards the epithecium, thecium and hypothecium there is great uniformity in all apothecia, but as regards the remaining structures there is a great difference met with among the various lichen-groups. The appearance also varies greatly according to the portion of the apothecium examined. If we examine a vertical section through the free portion of the cup of an apothecium (of *Parmelia*, for example) we shall find the following additional tissue-layers to be described:

(*d*) *Upper Algal Layer.*
(*e*) *Medullary Layer.*
(*f*) *Lower Algal Layer.*
(*g*) *Cortical Layer.*

(*d*) *The Upper Algal Layer.*

This layer occurs immediately below the hypothecium. In general it corresponds to the algal layer of the thallus; the algae are, however, less numerous and decrease in number from the periphery of the apothecium toward the middle; they are usually entirely wanting below the middle of the hypothecium; this is explained by the fact that at this point they are too far removed from sunlight.

(*e*) *The Medullary Layer.*

This corresponds in all respects to the medullary layer of the thallus. It consists of a network of hyphae which usually extend from the periphery to the middle of the point of attachment; near this point they extend downward toward the medullary layer of the thallus.

(*f*) *The Lower Algal Layer.*

This resembles the upper algal layer, but, as a rule, contains more algae. The relative number of algae in the two layers depends upon the inclination of the sides of the cup to the surface of the thallus; if this angle is large the lower algal layer will contain by far the more algae; if the angle is small the relative difference will be greater. This layer is continuous with the algal layer of the thallus.

(*g*) *The Cortical Layer.*

This layer is a direct continuation of the upper cortical layer of the thallus; it may, however, differ considerably from this in thick-

ness and structure. As a rule, it is thicker, as is well shown in *Omphalaria*, *Leptogium* and other genera. This is for the purpose of affording the additional mechanical support required, as well as of aiding in the ejection of spores. The cells of this layer retain the same relative position they had in the thallus; so that the ends which pointed upward in the thallus now point downward or diagonally outward.

The four layers described always occur in apothecia with typically developed thalloid exciples. The algal layers never occur in the so-called "excipulum proprium," or proper exciple. The medullary and the cortical layers may be present, but even these reach their highest development in the apothecia with thalloid exciples. We can readily understand the structure and development of the thalloid apothecium by comparing it with the thallus of the flattened fruticose lichens—*Cetraria*, for example; in this group we find that the thallus contains the following layers: 1, cortical; 2, algal; 3, medullary; 4, algal; 5, cortical. That is, the apothecium presents a "centric" thalloid structure, if we compare epithecium, thecium and hypothecium to one of the cortical layers of the thallus; its mode of development is likewise essentially the same as that of the centric fruticose thallus. The absence or presence of algal layers in the apothecia leads us to recognize two types which we shall discuss somewhat in detail.

2. TYPES OF APOTHECIA.

(*a*) *The Fungal Type.*

This type occurs in nearly all crustaceous lichens and in some of the foliose forms. The apothecium contains no algae and in the lowest form no part of the thallus enters into its formation; in all essentials it is like the apothecia found among the Ascomycetes. It consists of a thecium and hypothecium; the margin of the hypothecium forms the proper exciple; hypothecium and exciple form the perithecium in the closed apothecia. The term perithecium is not employed in reference to open discoid apothecia.

(*b*) *The Thalline Type.*

This always contains symbiotic algae; its structure has been sufficiently explained in the discussion of the apothecia.

It is very difficult to draw a dividing line between the two kinds; all gradations being found between the simplest fungal type and the most highly developed thalline type, nor is the matter simplified by further subdividing the apothecia as Nylander and others have done. I have designated as thalline all apothecia in which there is unmistakable evidence that the algae enter into the formation of the exciple; this leaves a large number of apothecia which must be classified with the fungal type in which the cortical and medullary layers of the thallus aid in forming the exciple.

I have purposely avoided employing technical terms referring to the different parts of the exciple, such as *pars marginalis*, *margo proprius*, *pars thallina*, *exipulum zeorinum* as well as the terms referring to apothecial type-variations. It is hoped that the description of the typical apothecium and the comparison of the fungal and thalline types will make clear to the student the variation of the apothecium in its phylogenetic development.

3. THE SOREDIA.

Structurally, the soredium proper is a spherical body consisting of from one to many algae surrounded by a continuous hyphal tissue; functionally they are the chief vegetative propagative organs of lichens. They are in a certain sense the typical reproductive organs, since the spores, in themselves, are wholly incapable of developing into a new lichen. Each soredium contains both symbionts in a suitable relationship for developing into a new lichen as soon as favorable conditions present themselves; they might be compared to miniature lichen-thalli, as will be evident from a study of their morphology as well as their development.

Soredia are more or less common upon the upper surface and margin of most of the higher lichen-thalli. They take their origin from the algal layer at points where the upper cortical layer is broken; they are sometimes quite uniformly distributed over the entire surface of the thallus, giving it the appearance of being covered by pollen dust; they occur very rarely upon the lower surface. The soredia are formed as follows: A hypha of the algal layer still adherent to an alga, if it occurs near the above mentioned breaks in the cortical layer, begins to form additional branches or haustoria which enclose the alga; in time the alga is entirely enclosed by this hyphal tissue; more frequently a group of two or

more algae are thus enclosed, and in the majority of cases the alga or algae which are being enclosed by the hyphal branches divide so that the mature soredium contains a considerable number of them. The cell-walls of the enclosing hyphal tissue become considerably gelatinized and closely agglutinated, thus forming a tissue especially adapted to prevent the evaporation of moisture. Each soredium is pushed outward by the elongating filament to which it is attached and others are formed below it; they are all loosely held together by the united hyphal filaments of the thallus; those uppermost are most loosely connected and are readily torn away by air currents. The distribution of soredia is analogous to the distribution of the pollen of anemophilous flowers. If the soredia fall upon suitable places they will begin to develop at once; if not they may lie dormant until the conditions are favorable for their development or they may be carried by the wind to some more suitable locality.

Each soredium may also develop other soredia producing the soredial dust which sometimes covers considerable areas; this happens where the surroundings are not favorable to the development of a thallus and yet not sufficiently unfavorable to cause the cessation of all growth.

Reference should also be made to the isidioid or warty soredial branches which occur on *Usnea* and on many foliose thalli; they are soredia which have developed into imperfect thalli upon the mother thallus, and are known as secondary thalli or phylloclades (Reinke). There is, however, no doubt that in many cases these secondary branches, which are comparable to leaves, are not developed from soredia, but are a direct product of the algal zone of the mother branch.

4. THE THECIAL ALGAE (HYMENIAL GONIDIA).

Among various groups of lichens, especially the Verrucariaceae, algae are found which regularly occur upon and about the constituents of the thecium; this is a constant occurrence in *Dermatocarpon* (*Endocarpon*) *pusillum*. In this case the algae are small and belong to the genus *Pleurococcus* (see *Dermatocarpon*). Füisting, Stahl and others state that these thecial algae are derived from the algae of the thallus. Due to a change in nutrition, the alga-cell of the thallus, on entering the apothecium, divides into a number of smaller cells, which adhere to the gelatinized paraphyses and to the walls

of the spore-sacs and further divide until nearly the entire apothecial cavity or cup is filled; many of them escape and are either destroyed, or continue to exist upon the thallus. Stahl has maintained that the thecial algae adhere to the spores, are ejected with them, and if they fall upon a suitable place the spores germinate and the hyphae enclose the algae, which then undergo a great transformation; instead of remaining pale green and small, as they were in the thecium, they regain the dark green color and size of the algae of the thallus. If his observations are correct it would seem to prove conclusively that the thecial algae play an important part as aids in reproduction. According to Reinke the spore with the adherent algae may be compared to a soredium, that is, we have the union of the essential elements for the formation of a new lichen, the fungal portion being represented by the spore. Structurally, they are the reverse of the soredia, the fungal portion (spore), being enclosed by the algae. As propagative organs they are less reliable than soredia, since the algae do not have the protective covering required to enable them to tide over unfavorable conditions for any length of time, as, for example, a want of moisture. If the spore, with the adherent algae, falls upon a dry spot, the algae would very probably die because of lack of moisture before the spore could develop; if subsequent moisture should enable the spore to germinate there would be no algae with which to enter into symbiotic association.

As already indicated, thecial algae are of wide distribution, especially in immature apothecia. In most cases they die before the spores mature and, therefore, can not have the biological significance that they do in *Dermatocarpon*. It is more properly a form of contingent symbiosis. The partially opened apothecial disk, no doubt, forms a suitable location for the algae, which are protected by the overhanging cortical tissue of the thallus or the exciple. As soon as this protection is no longer afforded, the thecial algae escape to some suitable locality, or fail to maintain their existence, owing to lack of moisture.

It is evident that the thecial algae are not always derived from the algae of the thallus, as may be seen from a careful comparative study. *Pleurococcus* seems to occur much more frequently than any other form of alga, particularly in a form closely related to *P. punctiformis*, if not identical with it. That the algae of the thallus should gain access to the apothecial cup is very likely, especially in those lichens with immersed apothecia (Verrucariaceae). Careful culture experiments are necessary to solve some of the undecided problems.

CHAPTER IV.

THE GROWTH, MECHANICS AND CHEMISTRY OF LICHENS.

INTRODUCTION.

In order that the student may have a better understanding of the special discussion of modes of growth and development as well as of mechanical adaptations, it is well to present a few explanatory statements, which will obviate the necessity of continually referring to the exceptions to the types of growth under consideration.

In the majority of lichens the fungal symbiont initiates and directs the mode of growth. The algae are entirely enclosed and take a position dependent upon the development of the hyphal portion as well as upon the requirements of assimilation. This position also controls their rate of growth and development in any lichen or in any area of the plant; in other words, there is a mutual adaptation of the two symbionts, so that the prime structural changes occur in the fungal portion and the prime functional activities are manifest in the algal portion. It seems as though there were some sort of agreement that one specialized portion should do the advance work in growth and supply the mechanical protection and support, while the other portion, by its highly specialized functional activity, should prepare the principal food substances.

In a few lichens, as *Ephebe pubescens*, the algal portion predominates and directs the mode of growth. It is, of course, evident that such lichens resemble the alga from which the algal symbiont is derived, and *Ephebe pubescens* is quite frequently classified as *Sirosiphon pulvinatus*; a careful microscopical examination only will decide whether the plant be lichen or alga.

There are also a few lichen-groups in which neither symbiont seems to predominate (examples: *Collema*, *Lichina*). In *Collema* we find hyphae and algae (*Nostoc*) almost equally intermingled; neither seems to take the lead in development, although there is considerable mutual adaptation.

I. GROWTH OF THE THALLUS.

(*a*) *The Protothallus* (*Hypothallus*, *Promycelium*).

As already indicated, the organ of lichens designated by the names protothallus, hypothallus or promycelium is, perhaps, morphologically unrecognizable; it will receive some consideration because in various works on lichenology it has been considered of great importance, especially in classification.

According to Schwendener the protothallus is the product of the spore and is said to occur only in crustaceous or scaly lichens, appearing as a hyphal tissue forming a fringe about the thallus proper. It usually differs from the thallus in color; it is most frequently black; the hyphae extend radially, that is, in the direction of growth of the thallus.

These observations of Schwendener are in the main correct, though their true significance is apparently not rightly understood. The protothallus is neither more nor less than the spore-product of the hyphal symbiont extending over the substratum. The hyphae form the apical growth of the thallus; the lower filaments extend into the substratum forming the rhizoidal network, the upper surround the algae at some distance from the margin. The color, which is usually well marked in old specimens, depends largely upon the substratum. In some cases there is a marked difference between the hyphae of the "protothallus" and the hyphae of the thallus, which seems to favor the belief that the protothallus is something foreign. It is quite probable that this doubtful structure is the hyphal network of a fungus preceding the growing lichen-thallus with which it has formed a symbiotic association; Minks believes that in many cases the protothallus is formed by the reduced host-lichen upon which some other lichen exists as a parasite.

No protothallus can be detected in mature higher lichens. The first product of spore development before it enters into symbiotic association with the algae has been designated as protothallus, especially by Schwendener. The term promycelium would seem more appropriate because of the fact that no thallus is yet formed. It can readily be understood that the term promycelium must likewise be variable and uncertain in its application. Sometimes the first hyphae come in contact with the algae immediately, sometimes not at all, in which case one of two things may happen; if it is a low form of lichen

(*Mycocalicium*, *Pyrenula*) it may mature as a fungus; otherwise it perishes.

Sufficient has been said to make it clear that the protothallus can have no definite morphological or physiological significance, and for that reason no great importance should be ascribed to it. There is no doubt that further study of this structure will clear up various phenomena yet unexplained or misinterpreted.

2. DEVELOPMENT OF THE THALLUS.

Two types or modes of growth may be observed in the thallus; (*a*), horizontal; (*b*), vertical; the former is met with in crustaceous and foliose lichens; the latter in fruticose forms.

(*a*) *Horizontal Growth.*

The increase of the thallus includes apical growth (marginal increase), as well as intercalary growth, that is, new cells are formed and existing cells increase in thickness and length; as a rule, new cells are formed at the apical areas, though new septa may be formed at any point of the hypha, especially toward the peripheral portions of the thallus.

In the lower crustaceous lichens the growing hyphae extend radially, parallel with the surface of the substratum. There is no evident distinction into apical areas, that is, marginal growth is uniform in certain forms. All of the hyphae, however, do not extend parallel with the substratum, since even in the lowest crustaceous types the rhizoidal hyphae extend vertically downward into the substratum. The stimulus which causes this downward growth (positive geotropism) is not understood, at least it has not been determined experimentally. The functional significance of the rhizoidal hyphae is very evident and has already been explained.

As soon as the thallus acquires any considerable thickness the hyphae of the thallus proper no longer continue exactly parallel to the substratum. Certain filaments extend downward and are continuous with the rhizoidal ones; some remain nearly horizontal (plagiotropic), while the upper have a tendency to become negatively geotropic. A vertical longitudinal section of such a thallus would show that the growing elements describe an orthogonal trajectory. The hyphal filaments turn upward and downward more and more as we proceed from the apex, so that they finally become vertical to the median plane.

In the higher crustaceous lichens and in all foliose forms, marginal growth is no longer uniform; certain parts show a more marked proliferation and are recognized as apical areas. It is evident that at these points the curves of growth are radial instead of in a single plane (vertical); the lateral curves are usually much the longest, and they do not terminate at right angles to the median plane. The rate and activity of apical growth determines the size and form of the thallus-lobes or of the thallus. Sometimes the upper hyphae curve more than the lower or *vice versa*, which causes the apical portion of the thallus to curve either upward or downward.

The differentiation of tissue elements begins very early in the development of the thallus. At a very short distance from the apex the tissues are fully formed and the thallus has reached its average thickness. On an examination of the apical area it becomes evident that the new cells are cut off at a short distance behind the apex, since the changes which they present are of secondary origin; they are shorter and their walls thicker than the normal hyphal cells, but longer and less differentiated than the cortical.

All gradations between the mode of growth of the lowest crustaceous lichens and that of the most perfect foliose forms can readily be found; to enter into a discussion of these multitudinous forms of growth is here unnecessary, as the descriptions of families and genera will do much to clear up points of detail.

(*b*) *Vertical Growth.*

As already indicated, fruticose thalli present either a centric or radial structure, and accordingly the mode of growth somewhat differs. Leaving out of consideration the question of direction, the development of fruticose thalli proceeds much as in horizontal thalli. The following are some of the differences: The apical areas are more clearly marked and more definite in their occurrence; branching is typically dichotomous, which, however, is also well marked in the higher foliose thalli, but indistinct or wanting in the lower foliose and crustaceous lichens; the apical areas are also less blunt, and the lobes or branches do not obtain their full thickness as quickly as they do in typically foliose lichens; the number of branches indicates the number of apical areas which had formed. No explanation has as yet been given of the main stem and branches taking their definite position. They are, no doubt, controlled by the same laws that con-

trol the direction of growth in higher plants. In a number of instances the secondary branches assume a position nearly horizontal, as in *Usnea barbata* and the apothecial branches of some *Cladonias*, but they are more frequently directed diagonally upward.

In this form of lichen growth the fungal symbiont likewise initiates and controls the mode of development: there are, however, notable exceptions, as we shall learn in the discussion of algal growth and development. It must also be borne in mind that in some lichens there is a combination of horizontal and vertical growth, as, for example, in *Cladonia*: this is more specifically an association of a foliose and a fruticose development. In *Cladonia* the so-called primary thallus is flattened: it develops in the manner of a typical foliose thallus, but the podetium is typically fruticose in structure and mode of growth. This peculiar difference of growth is readily explainable when we consider the phylogenetic development of the podetium: morphologically and physiologically this organ is a thallus, but originally it was no doubt an apothecial structure which during its phylogenetic evolution became converted into a thallus: it takes its origin endogenously from the primary thallus in the manner of apothecia proper; it grows from a single apical area and upon pushing its way through the upper layers of the primary thallus develops into a podetium with a typical radial structure. The podetium is of interest from a biological standpoint, since it gives evidence of the constancy of morphological characters. Although the present functional activity of the podetium is entirely thalloid, it has retained many of the morphological characters of the apothecium. For a more complete discussion of this subject see the excellent paper by Reinke (75, I).

(*c*) *Intercalary Growth.*

In intercalary growth new cells are interpolated and existing cells are increased in length and width. In general, intercalary growth causes the thallus to increase somewhat in surface expansion and in thickness. The interpolation of new cells is most active near the margin of the thallus, near the peripheral portions, and in the algal zone. The internal tissues, medullary hyphae and central conducting tissues, which are also mechanical are modified by the elongation of their cells. In the cortical layers and dermis of the foliose thalli the cells become shortened and their walls thickened:

lateral branches are also frequently formed, especially in the algal area.

Intercalary growth is slow in all parts of the thallus, with the exception of the apical portion; it is continuous, although the thallus soon obtains its full thickness; the oldest cells (dermal, rhizoidal) are continually worn away and replaced by new ones formed more internally. This process varies with the atmospheric conditions, but it continues as long as the plant lives.

Without exception, new septa are cut off transversely to the long axis of the hyphal filament. In general, it is true that the secondary changes affecting the longitudinal walls also affect the transverse septa. It is also reasonable to suppose that these secondary changes are simple and limited in accordance with the secondary changes in other lowly organized plants. The mechanical adaptations will be more fully discussed in another chapter.

II. GROWTH OF THE APOTHECIA

The apothecia, which resemble the spore-bearing structures of certain Ascomycetes, belong to and take their origin from the hyphal portion of the lichen. In stratified thalli the apothecium begins to develop beneath the algal zone; in the so-called homoemerous lichens at some point in the interior of the thallus. Its first appearance is noticeable as a rounded mass of irregularly interwoven hyphae; from this hyphal mass numerous vertical branches arise and constitute the beginnings of the paraphyses. The original hyphal network which forms the hypothecium increases in width much more rapidly than in thickness. The lateral proliferation does not, however, extend horizontally, but in a direction outward and upward, so that the hypothecium becomes concave above; and, as the hypothecium increases in width, new paraphyses are formed parallel to those already existing. While growth in the apothecium does not cease until it is fully matured, it decreases from the periphery of the hypothecium toward the middle; new paraphyses are occasionally pushed up between the others, especially near the periphery.

The spore-sacs begin to form very early in the development of the paraphyses; a terminal cell of a hypha enlarges and gradually pushes its way upward between the paraphyses; it can readily be distinguished from these structures by its greater size, the richness of its plasmic contents, and by the fact that it is always single-celled,

while the paraphyses have at least several transverse septa, as well as being branched in some cases. There is a difference of opinion as to the origin of spore-sacs, some authors (Schwendener, Fuisting) maintaining that in all cases they take their origin from a specialized hyphal tissue having no connection with the hyphae producing the paraphyses, this hyphal tissue being known as ascogenous hyphae, and always recognizable by its blue coloration with iodine after treatment with potassic hydrate. Other authors (Sturgis) deny the existence of a special ascogenous tissue. As far as my observations go it seems that the hyphae terminating in spore-sacs are different in structure from the hyphae from which the paraphyses are formed, being thicker and more irregular in shape. In most cases it was, however, impossible to distinguish such a tissue, either microscopically or by the aid of the iodine reaction. In no case could it be definitely proven that the spore-sac bearing hyphae were entirely distinct from those bearing paraphyses, both seeming to arise as branches from the same hyphal system.

As the apothecium increases in size it causes the superimposed structures of the thallus to bulge upward and finally to rupture. In immersed apothecia the opening thus formed in the thallus is small, while in lichens with free apothecia the superimposed tissue is removed, or remains in part in a fragmentary form upon the thecium (see Epithecium).

After the apothecium has broken through the thallus it may continue development either with or without concomitant changes in the thallus; in the one case the portion of the thallus immediately surrounding the true exciple grows with the latter structure, so that the mature apothecium is enclosed by a cortical, algal and medullary tissue continuous with that of the thallus, the growing apothecium no doubt acting as a stimulus which causes the surrounding area of the thallus to take on renewed cell-activity. In the other case the thallus is not affected by the apothecial growth, the apothecium simply forcing its way through the thallus and continuing to grow, sometimes developing a long stipe, on the top of which the apothecium is borne (*Calicium*, *Coniocybe*). There are all gradations between the forms in which the thallus takes no part in the formation of the apothecium and in which it even precedes the margin of the proper exciple. The thalloid exciple serves to increase the assimilative function, which is demanded by the increased cell-proliferation involved in the formation of the apothecium.

III. THE DEVELOPMENT AND STRUCTURE OF THE SPORES.

As far as has been observed, the spores of Ascolichenes are formed in the same manner as the spores of the Ascomycetes. As observed in *Pertusaria communis* the first stages of spore-formation are identical with those in the fungus *Peziza confluens* as recorded by De Bary. The earliest beginnings of the spore-sac as seen in *Pertusaria communis* are distinguishable by the more granular and richer plasmic contents of the sac as compared with those of the normal hyphal cells; as yet no nucleus is noticeable, but somewhat later this organ appears as a spherical transparent highly refractive body. With the growth of the spore-sac the plasmic contents advance more and more toward the apex; the upper portion of the plasm contains numerous small vacuoles; the lower portion contains few or none and is also less coarsely granular. The original nucleus now divides into two, these into four and finally each one again into two, thus making eight nuclei or spore mother-cells which in the majority of lichens take a position in a vertical row, and each becomes enclosed by plasm which is more translucent and granular than that of the spore-sac.

From this point developments differ materially, depending upon whether the mature spore-sac will contain the normal number of spores (eight) or fewer. In *Pertusaria communis* the number of mature spores is one or two; in this case it is found that only one or two of the spore mother-cells or nuclei will continue to grow, the remaining six or seven not developing, and finally becoming partially absorbed by the growing spore which in all cases is the one uppermost. As the spore increases in size, it assumes more and more its definite form; the spore-wall also makes its appearance quite early and increases in thickness and surface. As indicated above, the eight nuclei develop into mature spores in the majority of lichens; those arriving at maturity take a definite position within the spore-sac; in the majority of cases being placed diagonally across the sac parallel to each other. The elongated acicular and cylindrical spores usually extend longitudinally to the spore-sac and are often attached to a dense gelatinous mass near the apex (*Peltigera*).

Early in their development, all spores are simple and colorless and their septation whether in one or two planes, begins very early. This process requires further study. The coloring substances of spores may be deposited in the episporium (Caliciaceae) or uniformly

throughout the entire wall as well as throughout the septa. The spore-walls may also undergo other secondary changes; in the spores of *Pertusaria* peculiar thickenings of the endosporium are noticeable, which, no doubt, are for mechanical protection as well as to favor germination, the mechanical adaptation being required on account of their large size; germination of the spores begins at the thin areas. In other lichen-spores the exosporium is highly gelatinous, aiding them in adhering to the substratum in localities favorable for germination.

Oil globules are quite constantly present within the spores, and doubtless serve some purpose in the processes of germination. In some spores the plasmic contents are very coarsely granular, in others they are apparently quite homogeneous. It must be borne in mind that lichen-spores have undergone great structural as well as functional changes during their phylogenetic development. The spore-walls tend to become thinner and colorless; the septa have become irregular in occurrence and form, and the tendency is evidently toward simple spores. Many of the higher lichens are constantly without spores; the causes of such retrogressive changes will be discussed later.

IV. GROWTH OF ALGAE.

With certain exceptions the fungal symbiont constitutes the principal mass of the lichen and encloses the alga. In *Ephebe pubescens*, however, the alga (*Sirosiphon pulvinatus*) not only forms the bulk of the lichen, but it directs and controls the method of growth. In this lichen, growth proceeds from a single apical cell which forms two or more cell-rows; branching is distinctly dichotomous. The hyphae rarely extend to the apex; some branches may be entirely free from them.

In other lichen forms neither alga nor fungus seems to predominate (*Collema*) but the symbionts appear to be about equally distributed. In this group of foliose lichens the alga is a species of *Nostoc* in most respects similar to *Nostoc commune;* it occurs in chains loosely intermingled with the hyphae which do not form haustoria. The principal growth is marginal, that is, new alga-chains with heterocysts are continuously formed either from single cells or as branches from older chains. Certain marginal areas grow more rapidly than others, simulating apical growth and causing lobation or branching

of the thallus; the lobes or branches are, however, very irregular in their occurrence, true dichotomy not being recognizable.

In the majority of lichens the algae are entirely enclosed by the hyphal structure and their arrangement and development in the thallus is directed and controlled by the hyphal symbiont. This predominance of the fungal portion is, however, more apparent than real. We shall here consider only the arrangement and growth of the algae in the thallus; their structure and manner of division will be discussed in the chapter on Algal Types; their relation to the haustoria has already been explained.

In any given lichen the alga assumes its definite position as soon as the thallus has reached its mature development. The area of mature development begins near the apex, as has been explained. The rate of multiplication and distribution of algae keeps pace with the growth of the fungal portion. The position of the algae depends largely upon the form of the thallus or other structures (cephalodia, apothecia) in which they occur. To be more specific, it may be stated that the algae take a position most suitable for the utilization of sunlight and the exchange of gases resulting from the processes of assimilation. In the horizontal thalli (crustaceous and foliose) this is near the upper surface (bifacial thalli); in flattened fruticose thalli the algae occur in two layers, as both surfaces are nearly equally exposed to the sunlight (centric thalli); in radial fruticose thalli the algae are equally distributed on all sides. In the thalloid exciple they occur in two circular layers, and this exciple is therefore a combination of the centric and radial thalloid structure.

The active division of algae takes place near the apical areas; in the typically horizontal thalli they never extend below the apex; from that point backward they increase in numbers until the algal layer obtains its average thickness near the point where the thallus reaches its normal thickness. New algal cells are formed above and below a median horizontal plane through the algal layer. The limitation of growth in thickness of the algal layer is determined by several influences, first of all, by the requirements of assimilation; secondly, by the thickness of the superimposed structures of the thallus. New cells are continually formed in the lower zone of the algal layer, while the older ones in the upper zone die and the empty cell-walls are carried upward by the growing hyphae and become intermingled with the protective coverings of the thallus. In general,

however, algal cell-proliferation is very much retarded in the fully developed portions of the thallus. The arrangement of the algae into distinctly marked layers is simply the morphological expression of the assimilative function in its relation to the lichen-structure as a whole. In general the analogy between typical foliage leaves and lichen-thalli is so striking that the student will have no difficulty in comprehending the relative functional activities of the various structures.

V. THE SPERMAGONIA.

The spermagonia are minute structures occurring upon the thallus of many lichens and are usually more numerous near the margin of the thallus. They resemble certain little known structures met with in fungi and are similar to the spermagonia of *Aecidium*. They appear as minute black cups sunk into the upper surface of the thallus, opening by an apical pore. The sterigmata upon which the spermatia are borne are formed internally; the latter are slender acicular straight or curved spore-like bodies, which at maturity escape from the pore.

As has been stated, Stahl, and more recently Sturgis, looked upon the spermatia as the male reproductive organs of the collemaceous lichens, but in spite of their trustworthy observations other investigations would seem to indicate that the spermagonia are neither more nor less than parasitic fungi of which the spermatia are the spores. DeBary has clearly shown that the spermagonia of certain fungi are true parasites. It has also been repeatedly observed that the spermatia will develop into a mycelial network. From a comparative study it seems probable that the spermagonia are fungi allied to the genus *Septoria*. For example, *Septoria Specularіae* presents the general morphological characters of most spermagonia. In the case of this fungus the morphological and physiological contrasts between host and parasite are great, while in the case of the spermagonia these contrasts are only slight. It was impossible to demonstrate that the hyphae of the spermagonia are organically continuous with the tissue of the lichen.

For the sake of completeness, we will briefly explain Stahl's conception of reproduction among certain lichens (*Collema*). The first beginning of the apothecium takes its origin from medullary hyphae near the middle of the thallus; it consists of a colorless hyphal branch, rather thicker than the normal hyphae, which after form-

ing a coil extends vertically upward so that the free end projects somewhat above the surface of the thallus; the entire structure is known as the carpogone; the spiral coil as the ascogone and the free cone-like end as the trichogyne. The carpogone is supposed to be the female reproductive organ. The male fertilizing element (spermatium) escapes from the male receptacle (spermagonium) and is carried to the trichogyne by water-currents (rain, dew, rarely running water), whereupon it adheres to the conical projection for the purpose of fertilization. As soon as fertilization is completed the ascogone begins to develop into the apothecium; the ascogone enlarges and becomes flattened, forming the sub-hymenial layer, from which the spore-sacs develop; the paraphyses arise from a distinct hyphal tissue lying near the ascogenous tissue. Stahl's observations have been seconded by Sturgis. The latter author recognizes two forms of the sexual process, the one "characterized by the transformation of the spermagonium into an apothecium after the fertilization of the carpogonium," by which he doubtless means that the carpogonium takes its origin in the receptacle of the spermatium; the other sexual method is "characterized by a complete separation throughout their entire course of development, of spermagonia and apothecia."

Some authors also speak of monoecious and dioecious lichens, in the former both sexual organs (spermagonia and ascogonia) occurring on the same plant. Only a few species are supposed to be dioecious (example: *Ephebe pubescens.*)

VI. MECHANICAL ADAPTATIONS.

On account of the great length of certain fruticose thalli and the great surface expansion of some foliose thalli (several feet or more) it is reasonable to suppose that there must be special mechanical tissues to resist the forces continually acting upon them. The forces to be resisted are either lateral or longitudinal. Longitudinal tensions may be either pulling or pushing (supporting). It must, however, be remembered that no mechanical tissue is wholly adapted to resist one given tension, that is, while a tissue is especially adapted to resist pulling tensions it nevertheless also resists lateral tensions as well as longitudinal compression (example: *Usnea barbata*).

In lichens the mechanical tissue is in most cases a product of the fungal symbiont. Besides its mechanical function it may serve as a

protecting, aerating or conducting tissue (cortical layers of foliose thalli: cyphellae: longitudinal bundles of hyphae). For convenience of description, the mechanical adaptations met with in lichens are divided into five types. Type I. Hollow Cylinder. Type II. Central Strand. Type III. Direct Guys. Type IV. Lateral Guys. Type V. Cap with Basal Ring.

Type I. Hollow Cylinder: Podetia of Cladonia. This form of mechanical tissue occurs also in *Alectoria*, *Bryopogon*, as well as in *Pilophoron*. Here are included all flattened thalli whether horizontal or vertical, which have both upper and lower cortical layers. Such a structure may be considered as a compressed cylinder, whose function is the same as that of the normal cylinder, namely, to resist lateral tensions. It is very evident that such mechanical tissues require filling material to prevent the collapse of the broad surfaces. This filling material is supplied by the medullary and algal tissues. The hollow cylinder consists of much elongated, sparingly branching parallel hyphae, which in cross-section appear as a continuous internal ring. The cells are very long and closely united. The typical mechanical hollow cylinder is without filling material. But if the cylinder is of considerable diameter and the tissue thin, special support is necessary to prevent collapse due to excessive lateral pressure. In *Cladonia* and other groups this is prevented by transverse bundles of hyphal tissue which extend at right angles to the lateral compressing force. These bundles are, therefore, subject to a pulling tension; they are also able to resist vertical (longitudinal compression) tensions, but to a much lesser degree.

The cylinder composed of longitudinal hyphal tissue may also be external, that is, outside of the algal layer as in *Theloschistes*, *Bryopogon* and *Alectoria*. This evidently makes it a more perfect mechanical structure but doubtless interferes somewhat with the function of assimilation.

Type II. Central Strand: Usnea barbata. This mechanical structure reaches its most highly specialized development in *Usnea barbata*. It also occurs in *Stereocaulon* and *Baeomyces* as well as in the stipes of Caliciaceae, but in these cases it is apparently not as highly specialized as a mechanical tissue. In *Usnea* the central strand serves to resist pulling tensions due to the weight of the enormously elongated branches. This structure, like the hollow cylinder, consists of much elongated, sparingly branched hyphal filaments

which extend parallel with the longitudinal axis; it is enclosed in *Usnea* by a tissue consisting of much modified, slightly colored hyphal cells, which may be termed a protective sheath analogous to the endodermis of vascular bundles in higher plants.

Under this form of mechanical tissue we must also include the elongated tissue-bundles met with in foliose thalli; as for example the "veins" near the lower surface of the thallus of *Hydrothyria venosa* and *Peltigera venosa* as well as the elongated hyphal groups occurring in different parts of foliose and fruticose thalli. From their structure and position it is evident that they serve to resist pulling tensions. It is, however, very evident that many fruticose thalli with solid cylinders are almost wholly subject to lateral tensions, as *Stereocaulon* and *Sphaerophorus*; this is explainable by the fact that more conducting elements are required than could be supplied by a thin hollow cylinder, and it is therefore functionally comparable to the solid tree-trunk. The same may be said of the stipes.

Type III. Direct Guys: Peltigera aphthosa.—Among the foliose thalli the cortical layers are not sufficient to give the necessary mechanical support and there must therefore be other adaptations to meet this requirement. This we find in the rhizoids which act as direct guys fastening the thallus to the substratum. *Peltigera aphthosa* is selected as the typical example because in this lichen the mechanical function of the rhizoids seems to have reached its highest development. All rhizoids (excepting the aerial ones) must, however, be included, although their prime function may be that of taking up soluble food-substances. Their mechanical significance is especially apparent in the higher foliose lichens, as *Physcia*, *Parmelia* and *Mallotium*.

The so-called "umbilicus" is a highly specialized mechanical adaptation belonging to this type, occurring typically in *Gyrophora* and *Umbilicaria*. From some point near the middle of the lower surface of the expanded thallus bundles of root-like hyphae extend by means of which the lichen is quite firmly attached to the substratum. The analogy, both as to structure and function, between the umbilicus and the roots of higher plants is striking, and will impress itself upon the student without further explanation. It must, however, be remembered that the homologue of the umbilicus is the rhizoid, and that it is phylogenetically derived from the latter structure; whether the mechanical function predominates over the physiological or not is undetermined.

Type IV. Lateral Guys: Gyrophora Dillenii.—These are other special mechanical adaptations met with in foliose thalli and are typically developed only in the above mentioned species. They consist of a cortical mechanical tissue extending from a central pillar to different points of the thallus, and their action is the same as that of the stays of an umbrella. The structure is due to a proliferation of the lower cortical layer and like that tissue consists of dark-colored cortical cells which do not, however, form a continuous layer; it is made up of four or five thin layers, one above the other, which are connected by vertical septa of cortical tissue (to prevent breaking due to lateral forces). There is little doubt that the prime function of this tissue is mechanical.

Type V. Cap with Basal Ring: Gyrophora pustulata.—Another highly specialized mechanical tissue is typically developed in *Gyrophora pustulata*. It consists of pustular elevations of the thallus, each one of which bears a basal ring of hyphal tissue. The pustules themselves constitute a mechanical structure formed by the cortical layers with the intervening filling material. This cap would, however, tear easily at the margin if it were not for the supporting ring. On an examination of this lichen it will be found that the largest pustules or caps occur where the greatest strain is exerted, that is about midway between the margin and center; on either side of this point they begin to decrease in size. The central portion of the thallus is attached to the substratum by the enormous umbilicus.

Mechanical adaptations belonging to type V. are also well developed in some of the Collemaceae. Under this type must also be included the foldings and pustules of thalli without mechanical rings as they evidently serve to resist lateral tearing forces; such foldings are well marked in some *Stictas*. In connection with the mechanical function of the pustules it must not be forgotten that they also increase the assimilative function by increasing the algal surface.

There are various modifications of the types here explained; the explanations here given are sufficient to enable the student to comprehend the significance of the mechanical adaptations met with in lichens.

VII. THE CHEMISTRY OF LICHENS.

There is considerable chemical activity accompanying the process of assimilation, going on in the lichen. Under the influence of sunlight, moisture, and a certain degree of warmth, the plant appropriates the CO_2 of the atmosphere and in return gives off O. In

this function it is in all respects similar to the foliage leaves of higher plants. Jumelle (44) has shown that the variation in the function of assimilation is much greater in lichens than in higher plants ; also their adaptability to extremes of temperature. Assimilation varies greatly in the different lichen-forms. There has been observed an optimum of moisture ; increasing the degree of moisture above this point reduces transpiration, as does also reduction below the optimum. The extremes of temperature at which assimilation is still perceptible are between —40° and 60°C. A temperature of 60°C. will, however, destroy life, in some lichens in about one hour.

The most important substance is no doubt lichenin or lichen-starch, whose chemical formula is the same as that of cellulose and starch ($C_6H_{10}O_5$). It occurs more or less plentifully in all lichens. In the higher types it constitutes from 40% to 65% of the bulk. It forms the principal constituent of the cell-walls. This substance absorbs moisture very readily, but is comparatively slow to lose it. It also becomes more or less gelatinized in different parts of the plant, especially in the cortical tissues and walls of the spore-sac. The chemical behavior of lichen-starch is essentially different from starch or cellulose ; it rarely gives the blue coloration with iodine, as in spore-sacs and parts of the hypothecium. A strong solution of potassium hydrate dissolves the cortical cell-walls of many lichens, and causes all of them to swell considerably without producing any coloration in the colorless hyphae. In the colored cell-walls this reagent may produce brilliant effects, usually reddish or purple. Nylander states that lichens also contain true starch-grains intermingled with the tissue-elements, but this observation has more recently been proven to be erroneous.

Other important chemical constituents of many lichens are coloring substances deposited in the cell-walls in various parts of the lichen, especially in the outermost layers of the cortical tissues, in the upper ends of the paraphyses and in the hypothecium. Sometimes granules of coloring substance (usually acid crystals) are deposited on the outside of the hyphae, as in *Solorina*. The prevailing colors are yellow, red, brown, dark-brown or black. The most important of these coloring substances is orchil (orseille, cudbear) which occurs most plentifully in *Rocella tinctoria;* in extracting it the lichens are finely ground and leached in a solution of ammoniacal potash until the lichen-mass takes on a purple color. The forma-

tion of the color is explained as follows: Most lichens contain colorless acids free from nitrogen, such as erythrinic acid (formed by the union of erythric acid with erythrite), orsellinic acid, etc., which are very readily transformed into orcin [$C_7H_6(H_2O)$]; in the presence of an alkaline solution, as ammonia, the colorless crystals of orcin are dissolved, forming a purple solution known as orchil. Litmus is a special preparation of orcin which changes to red in the presence of acids and blue in the presence of alkalies; for this reason it is extensively used in making chemical tests, litmus paper being ordinary bleached paper dipped in a solution of litmus. Orchil is also used by artists as a pigment.

Lichens contain a number of chemical compounds which are but little understood and for that reason will not be discussed. Many of them evidently depend upon the chemical nature of the substratum.

Oil globules are quite common in the spores, less common in the hyphal cells. The rhizoidal "fat cells" in calcareous lichens have already been mentioned. Calcium oxalate crystals are of common occurrence in different parts of the lichen, being most frequently found in the higher foliose species. The more or less imaginary tonic and antifebrile properties of many lichens are due to the bitter extracts (acids, etc.) which were obtained from them. The nutritious properties are of course due to the large percentage of lichenin.

The dark rusty coloration met with in many lichens, particularly in crustaceous forms, is due to an infiltration with some salt of iron (Gümbel).

The microchemical examination of lichens reveals the fact that their chemical compositon is variable, depending to a large extent upon the substratum upon which they live. No chemical test is absolutely reliable. In general, it is, however, found that a blue coloration of the thecium with iodine takes place in most of the higher lichens; in many of the lower forms, as *Baeomyces*, it does not; and while some respond very quickly to this reaction, others are very slow. All lichenologists have noted the extreme variability in the amount of coloring substance of orchil-producing lichens (*Rocella*, *Pertusaria*, *Gyrophora*, etc.). Our knowledge of the chemistry of the lichens is very deficient, notwithstanding the voluminous, though fragmentary, literature on the subject.[1]

[1] Most of the publications on the chemical constituents of lichens are to be found in the chemical journals. (Erdmann's Journal für practische Chemie. 1846—). No recent important chemical analyses have been made.

CHAPTER V.

REPRODUCTION AND PROPAGATION OF LICHENS.

In the discussion of this subject only the established facts will be considered. The hypothesis of the sexual origin of apothecia and spores has already been briefly discussed, but it has been sufficiently dwelt upon to enable the student to realize the confusion that has been created in the systematic part of lichenology by ascribing to the "male sexual organs" properties which they perhaps do not possess, and of making them almost coequal with the spores as a basis for classification.

It is also well to anticipate a little by calling the student's attention to the fact that structures of different groups of plants which are morphologically similar may differ widely functionally. Such are the spores of fungi and lichens. These great functional differences of organs which are almost identical morphologically will be explained in the discussion of lichen-spores, to enable the student to realize why they are considered of such great importance in the system of classification, while they are very unimportant physiologically.

I. THE SPORES.

1. THE EJECTION AND DISTRIBUTION OF SPORES.

There is little or no difference of opinion concerning the method of the ejection and distribution of spores among lichens. Tulasne has already recorded exact observations as to the manner in which they are ejected and still more complete observations were made by Ohlert. Both authors agree that the turgescent state of the hypothecium and excipulum, aided no doubt by the paraphyses and the gelatinous substance within the spore-sacs, produce the required mechanical action to force the spores out of these organs. The spores escape from the apex of the spore-sac by the rupturing of the apical wall; sometimes a cap-like segment is torn across, as in *Pertusaria* and other genera. The method of opening or rupturing is by no means constant in a given group or even in a given plant or apothecium. As already stated, in the Caliciaceae the upper portion of the spore-sac is entirely dissolved even before the spores are

matured; and in this family they are not ejected to the exterior because of the closed perithecium and exciple, but are retained in the space above the thecium, where they mature; later, the perithecium opens by an apical chink or pore, thus allowing the spores to escape.

A very simple experiment will illustrate the forcible ejection of spores. By placing fresh spore-bearing lichens in a moist chamber and laying a cover-glass over the apothecia it will be found in a few hours that the cover-glass contains numerous spores which have been propelled against it. Tulasne and Ohlert have estimated that the spores may be projected to a distance of more than two centimetres. On examining the slip bearing the ejected spores it is found that they occur in groups in which the prevailing number is eight, as the majority of spore-sacs bear eight spores; this grouping is due to the fact that the spores are held together by a gelatinous substance which compels them to escape at the same time. This gelatinous substance is especially apparent in spore-sacs bearing numerous spores, as *Biatorella* and related genera; sometimes the exosporium is very gelatinous and swells enormously when moisture is added; this no doubt serves the purpose of aiding in their expulsion as well as in enabling them to adhere to any suitable substratum.

The spores of the entire apothecium are by no means all ejected at the same time, dissemination continuing for a long period under favorable conditions, as during showers, damp weather, or dews. Neither are the spores of one and the same apothecium all matured at the same time; for an examination of sections of various apothecia shows mature spore-sacs associated with others just beginning to form; this, in a measure, explains the long period of spore-ejection.

While the spores are ejected during moist periods their distribution takes place mainly during dry periods. On ejection the spores either fall back upon the disk of the apothecium or in its immediate vicinity, especially upon the surface of the thallus. During periods of dryness they lose much of their moisture, the gelatinous substance shrinks and becomes hard, and the entire spore-substance becomes lighter, thus enabling air-currents to distribute them more readily.

From the comparatively insignificant part that spores play in the process of reproduction it is not reasonable to suppose that there are many structural adaptations favoring their distribution. All the extensive phylogenetic adaptations in the apothecium are primarily in favor of an increase in the function of assimilation; such are the

various modifications of the thalloid exciple and the podetia of *Cladonia* and *Thamnolia*. The form of the thalloid apothecial cup favors the function of assimilation rather than the distribution of spores, yet there are a few apothecial adaptations which would seem to aid in this process. In *Nephroma*, for instance, the apothecia occur on the lower surface of the thallus; in the early part of its development the thallus-lobes lie horizontally flattened and no doubt afford a protection to the developing apothecium; when the spores are maturing the thallus-margin is turned upward at an angle of usually less than 90°, rarely more; the mechanical force is supplied by the excipular margin which increases in thickness more rapidly than the opposite (superior) cortical layer which is passively bent; with apothecia in this position the ejected spores are least liable to adhere to the apothecial disk and are readily acted upon and carried away by air currents. In *Parmelia perforata* we find very large cup-like apothecia, and it is evident that the majority of ejected spores must remain in the cup if no provision were made for their escape; this, however, is provided for by an opening at its base.

With these perhaps doubtful exceptions there seem to be no special adaptations for the distribution of lichen-spores. It must also be borne in mind that the adaptations for the ejection of spores are not derived during the phylogenesis as lichens, but are a direct acquisition and transmission from the fungal ancestor.

2. THE GERMINATION OF SPORES.

The germination of spores has been investigated by various authors, especially with a view to studying the relation of the spore product to the gonidia. We shall here limit our observations to the development of lichen-spores in general, without discussing their relation to the algal symbiont.

If the spore falls upon a suitable nidus it prepares for germination, either at once, or not until after a period of several weeks or months. A definite amount of moisture and warmth is all that is required, as the spores contain within themselves a sufficient quantity of stored food substances to allow the formation of the "promycelium" or "protothallus."

The initial changes observed are as follows, and occur in all germinating spores: The spore increases somewhat in size, the plasmic contents become more granular, the oil-globules are emulsi-

fied and no doubt serve a purpose in the metabolic processes of germination; soon after a projection may be noticed at one end of the body, and in some simple spores several or many of these projections may be formed nearly at the same time; the exosporium ruptures and the hyphal development begins. In the many-celled and multilocular spores each cell may develop a hyphal branch.

The initial hypha grows quite rapidly under favorable conditions and soon sends out lateral branches; about this time transverse septa are also being formed. This first hyphal network, known as the "promycelium" or "protothallus," consists of filaments more irregular in size and form than the later growth and the cell-walls are also thinner. If the promycelium comes in contact with the required algae the formation of the thallus begins as already described; if not, it perishes for want of the necessary nutrition.

The germination of spores can readily be observed upon glass slides kept in moist chambers. The greatest difficulty encountered is the development of bacteria and hyphal fungi which soon stop the lichen development. It should also be remembered that the growth of lichens may be materially checked or entirely inhibited by excessive moisture. As already indicated some spores germinate much more readily than others; those of *Dermatocarpon pusillum* usually begin development in a day or two; those of *Parmelia rudecta* require a much longer time. It is also necessary to select fresh material; spores of herbarium material several years old will generally fail to germinate.

3. SPORES AS ORGANS OF REPRODUCTION.

As to the phyletic origin and structure of lichen-spores there is uniformity of opinion; they are derived from and are structurally almost identical with the spores of certain ascomycetous fungi. But as to the true significance of these spores as organs of reproduction, there is considerable uncertainty and difference of opinion manifest. The true function of lichen-spores may readily be understood if one has a correct understanding of the lichen as a whole, or as a unit. As will be explained in the chapter treating of the polyphyletic origin of lichens, the lichen-spores are structurally very similar to fungal spores; physiologically they are, however, wholly different. *The spore of the fungus can in all cases develop into a new individual, while the spore of the lichen can not.* The reason is evident, for

the spore can produce only the fungal symbiont, but the fungal symbiont alone does not form a lichen, nor can it develop to maturity (with perhaps some exceptions). This seems to indicate conclusively that lichen-spores can not be considered as true reproductive organs.

The question now resolves itself into what part, if any, do lichen-spores play in reproduction? The explanation of the function of the thecial algae will suggest the answer to this question, that is, the spores at most only aid in the process of reproduction. The hyphae resulting from the process of germination must be biologically associated with the symbiotic algae before a lichen can be formed. The spores can indeed germinate without being associated with the algae, as has been proven time and again in culture experiments, but they can not develop a mature spore-producing structure without being united with the essential algae. There may be exceptions to this rule in the lower Caliciaceae, for example in *Mycocalicium*, which is a very questionable lichen genus, since it frequently happens that no trace of a thallus can be found; its species are perhaps true fungi. The same may be said of some species of *Pyrenula* and *Pyrenastrum*.

On further consideration it becomes evident that the spores are very unreliable even as aids in reproduction. Since the spores are distributed by air currents, it is also evident that their falling upon a locality in which the required symbiotic algae occur must be purely accidental. Even if this accident does happen, there is only a slight chance for the formation of a new lichen, for several reasons; the spore may not be ready for germination; in the meantime unsuitable climatic conditions may destroy the algae; and if the spore subsequently develops, there may be no algae with which to enter into a symbiotic relationship and as a result the "promycelium" dies.

Another problem of great scientific importance is to find the true relation of different lichen-spores to one and the same algal symbiont. As already explained an algal form closely related to *Cystococcus humicola* occurs in the majority of Ascolichenes. The important question for consideration is to find whether the various spores of lichens in which this alga occurs can develop into new lichens if brought in association with the alga of *Parmelia perlata* or any other alga selected from the group of the lichens mentioned. Some experiments which have been made in regard to the synthesis of

lichens make it seem probable that such is the case, but further careful observations are, however, necessary to give a satisfactory solution of this problem.

Germinating spores no doubt frequently enter into a symbiotic association with the soredia which are likewise promiscuously distributed by the wind. In these cases it would also be interesting to know whether the promycelium of *Physcia stellaris*, for example, can enter into a symbiotic association with the alga or algae of a soredium derived from a species of *Parmelia* or any other soredium in which the algae are *Cystococcus humicola*.

From the foregoing we may safely conclude that the spores of lichens are not perfect organs of reproduction, and that they are very unreliable as aids in reproduction. They can be looked upon only as the *degenerate reproductive organs of their fungal ancestors*. If this be true there must be some evidence of such degeneration. This evidence we actually find, especially in the higher phyletic series. For example, in the more highly developed *Parmelias* the spores are few or wholly wanting, as likewise in the higher *Cladonias*; in *Thamnolia* spores are always wanting. Some general signs of spore-degeneration besides their less frequent occurrence or total absence are decrease or absence of coloring substances in the spore-walls, indistinct septa, thin spore-walls; simple colorless thin-walled spores occur also in the lower lichens but are much less common than in the higher types.

II. THE SOREDIA AS PROPAGATIVE ORGANS.

The origin and morphology of soredia has already been discussed, and we shall here confine ourselves to a consideration of their special importance as reproductive organs. They are phylogenetically derived lichen-structures and are in a certain sense the typical reproductive organs of lichens. Morphologically it is, however, more correct to designate them as symbiotic propagative organs, functionally comparable to the vegetative propagative organs of higher plants. They are the only specialized propagative organs of lichens capable of developing at once into a new plant.

The mode of propagation by means of the soredia is very simple. As soon as a soredium is carried to some suitable locality development begins; the surface nearest the substratum sends out hyphal branches which enter the substratum for the purpose of taking up

soluble food-substances, as well as for the purpose of forming a firm attachment; about the same time the portion opposite the substratum undergoes considerable change; the hyphal cells forming the soredial covering elongate, the enclosed algae multiply by division and are carried upward by the elongating cells to which they are adherent. In all respects it resembles apical growth in the lichen-thallus; it is in fact the beginning of the thallus, from which in time the various tissue layers are differentiated. In the formation of all soredia the hyphae precede and direct the development of the enclosed algae. The plate illustrating the formation of the ectotrophic cephalodia of *Peltigera aphthosa* will also serve to illustrate the growth of a soredium.

Each soredium is capable of developing into a mature lichen bearing perhaps apothecia and soredia, as well as the other lichen-structures. Sometimes two or more soredia unite to form one thallus, this happening quite frequently among the *Parmelias* and other foliose species. As already indicated, the soredia may develop upon the mother-plant, especially upon the older and dying portions, where they produce the peculiar isidioid outgrowths, especially noticeable among foliose lichens. The numerous sterile vegetative branches of *Usnea* are, perhaps, also soredial products.

As to the relative value of spores and soredia as organs of reproduction, there can be little dispute. The soredia are by far the more important; many lichens are almost entirely dependent upon the soredia for propagation, as is evident from the fact that no spores are ever developed. It is also probable that lichens, which produce spores quite constantly, are regularly propagated by means of the soredia. From the very nature of lichens, spores can play only an insignificant part in the maintenance of the species.

There is another form of multiplication which is no doubt of less frequent occurrence than propagation by means of the soredia, but still more important than reproduction by means of the spores, and that is typical vegetative propagation, which will now receive brief mention.

III. VEGETATIVE PROPAGATION.

Any portion of the lichen-thallus may become detached and develop into a new lichen, provided the fragment contains both symbionts. Even the entire thallus may be torn away and carried to

some other locality, where a portion of it will develop into a new individual; this happens quite frequently among the higher crustaceous lichens, especially the *Lecanoras*. *Lecanora ventosa*, for example, is only loosely attached to the substratum; during dry periods large masses of this lichen are torn away and scattered by the wind, and, falling upon other suitable localities, they again begin growth.

Another and perhaps more frequent method of vegetative propagation is by means of the soredial branches (including warts and isidia) and thalli (secondary thalli). Typical soredial branches are very numerous on *Usnea barbata*. These structures, sooner or later, become detached and develop into new lichens very much in the manner of soredia.

Some lichens also possess what may be designated as continuous rejuvenescence, that is, there is unceasing apical growth accompanied by a continuous dying away of the basal portion. This phenomenon occurs typically in the higher *Cladonias* as well as in *Thamnolia*, and is also met with in some foliose lichens, as *Parmelia*. The central, hence older, portion dies away, while the margin continues to grow producing an appearance not unlike the "fairy rings" of certain mushrooms.

IV. LIFE PERIOD OF LICHENS.

No reliable observations have as yet been made as to the life-period of the individual lichen. It is supposed that some species live on indefinitely, as for example the *Cladonias*, *Thamnolia* and some of the foliose lichens; it has been roughly estimated that many *Cladonias* are hundreds of years old. Among the lower crustaceous lichens it is difficult to make any estimates as to the age of the individual plant, because we can not determine the limitations of its growth.

In general, it may be stated that lichens are perennial land-plants of comparatively slow growth. Meyer, whom we have already mentioned in the historical review, states that from actual measurements he has found that *Physcia parietina* grew six lines in six years when in a protected position and twelve to fourteen lines when growing on the weather side of a tree. *Lecidiella sabuletorum* upon sandstone grew two lines in diameter in four years. *Aspicilia cinerea* on the same substratum grew two lines during the same period. Since the thalli of the above lichens attain very large diameters, it is evident that they must become very old.

Wallroth has also made some observations on the growth and duration of lichens. According to this investigator the homoeomerous lichens (Collemaceae and Parmeliaceae in part) are of quickest growth and shortest duration; some of them may begin growth from a soredium and develop to maturity in the same year. He believed that the heteromerous lichens (Physciaceae, Parmeliaceae) were endowed with almost eternal life.

It must also be borne in mind that the growth of lichens is intermittent. During warm moist seasons it is comparatively rapid; while during dry periods and extremely cold seasons growth is reduced to a minimum; the limitation of the life-period must, therefore, be quite variable.

One remarkable thing in the life-history of lichens is the readiness with which these plants vanish before the progress of civilization. Trees (large as well as small) growing in the city parks, along much travelled roadsides, or in areas which have been under cultivation for a long time, bear only a few of the lower forms (*Lecidea*, *Graphis*, *Biatora*, etc.); the higher types being almost entirely wanting. This is evidently not due to mechanical interference, but it is, perhaps, owing to the detrimental influence of the fine dust which is everywhere stirred up in such situations. Rock-lichens are the last to disappear.

CHAPTER VI.

THE POLYPHYLOGENY OF LICHENS.

I. INTRODUCTION.

There is no doubt that the manifold variations observed in the development of lichens are adaptations in favor of the function of assimilation. We have also seen that lichens considered from a purely physiological standpoint resemble the lower chlorophyll-bearing plants (algae), but considered from a superficial morphological standpoint the majority of them resemble the ascomycetous fungi. It is now our purpose to discuss the phyletic relationship of lichens to the fungi and algae.

Upon careful examination it becomes evident that all forms of lichen can not have originated from a single fungal ancestor entering into a symbiotic association with a single species of alga, that is, it seems evident that their origin is polyphyletic and not monophyletic. Briefly stated, this means that the various phyletic series or branches took their origin from different fungal ancestors or types in association with certain algal ancestors. To study out the ancestral fungal types is at present impossible for several reasons; first of all, it is more than likely that the species of fungi which originally entered into the formation of the lichen-types no longer exist in their original form; that is, they have been converted into other forms or have most likely gone out of existence. It seems quite reasonable to assume that they have gone entirely out of existence as they were apparently dependent upon the symbiotic association for their maintenance. It must also be remembered that the fungal portion of the lichen has undergone considerable structural as well as functional change during its phylogenetic history. Both of these factors just mentioned make it impossible to determine the exact fungal ancestors, and this is especially true in the case of the higher lichens. We can, however, in a general way, determine what comprehensive groups of fungi resemble more or less closely the ancestors which entered into the formation of the lichen-types. The exact limitation of a given phyletic group of lichens is very uncertain, since we can not always determine how frequently a species may have changed its

algal symbiont during its phylogenetic history; for example, *Sticta* and *Stictina* doubtless originated from the same fungal symbiont but after a time *Stictina* formed a new natural branch by adapting itself to a different alga. Similar conditions are met with in other groups.

Just when, how and why lichens took their origin is not definitely known. The palæontologic record leaves us practically without data, so we are obliged to content ourselves with theoretical and hypothetical assumptions; these assumptions bear, however, the stamp of certainty, though they are incapable of direct proof. In a certain sense the probable conditions were very peculiar; it is now generally admitted that the various groups of fungi have had a polyphyletic origin from various algal ancestors; a change in the environment has doubtless influenced the chlorophyllian function in certain algae which adapted them to lead a parasitic life, and subsequently these same organisms again found themselves placed in a position favorable to or requiring carbon-assimilation, but having lost their chlorophyll they entered into a mutualistic relationship with algæ which could perform the required function.

Concerning the oldest types of lichens as well as the relative ages of the various phyletic groups, nothing definite is known. Reinke assumes that *Collema* perhaps represents the prototype; there are, however, no data to show that *Collema* is older than *Parmelia* or *Cladonia*. No authentic observations have as yet been made on the variability of lichen-species nor has it been possible to indicate the relative rate of phylogenetic evolution of the different groups. The question of variability is of great importance; that the species are very variable is generally known, but no one has as yet determined the limitations of such variation. It is very necessary that these limitations should be known before any reliable system of classification can be established, and observations on the variability of lichens will also throw light on the question of their phyletic evolution.

II. THE FUNGAL TYPES.

Upon one point all scientific lichenologists are agreed, and that is that the fungal symbionts of the *Ascolichenes* are derived from the *Ascomycetes*. It is also quite universally agreed that various lichen groups are represented by different groups of fungi, but for reasons already stated it is impossible to ascertain the exact fungal ancestors.

We must content ourselves with a consideration of the groups of fungi (families) from which the various phyletic series of lichens were most likely derived.

1. *The Pezizaceae.*—There is considerable morphological evidence that the fungal portion of the Caliciaceae is derived from some ancestral form or forms of the Pezizaceae. Although the generic groups of the Caliciaceæ are closely related it is not likely that they are derived from a single fungal ancestor; *Acolium*, for example, which, as a lichen is but little higher than *Calicium*, is very probably derived from a different fungal group, as seems apparent from the absence of the stipe. In the lichens of our territory there is a wide gap between *Acolium* and *Sphaerophorus*; the representatives of the latter genus are certainly highly developed as lichens and it is wholly impossible to determine the exact relation of their fungal ancestor to the fungal ancestor of *Acolium*. Its apothecial and spore-characters indicate, however, that it is derived from the Pezizaceae.

It must also be remembered that the evolution of lichens has no essential relation to the evolution of the ancestral fungal forms. The Caliciaceæ doubtless form the lowest group of lichens, but their fungal ancestors are derived from almost the highest group of the Ascomycetes.

2. *The Patellariaceae.*—The fungal ancestor of the majority of lichens is derived from the Patellariaceae. This large group of Ascomycetes differs from the foregoing in the absence of a stipe. The apothecia are discoid and sessile upon the mycelial network. Not only are the various lichen-families derived from different groups of the Patellariaceae, but likewise the various generic groups of lichens. In the family Physciaceae it seems probable that the different genera form a natural series derived from a common fungal ancestor; this, however, is a mere conjecture and is impossible of proof. In still other instances several lichen-genera are doubtless represented by a common fungal ancestor as *Collema*, *Leptogium*, *Mallotium* and *Hydrothyria*.

3. *The Phacidiaceae.*—The fungal ancestors of the Graphidaceae are no doubt derived from this family of the Ascomycetes. The apothecia are small, irregular in outline or linear, or rarely discoid (*Rocella*). The fungal symbiont of *Graphis* is very likely derived from the genus *Hysterium* as is indicated by the spore as well as the apothecial characters.

4. *Stictidaceae.*—Just how extensively this group of fungi is represented among the lichens is impossible to determine. Very likely *Thelotrema*, *Urecolaria* and *Gyalecta* find their fungal ancestors here, but further investigation is necessary to demonstrate the correctness of this supposition.

5. *The Sphaeriaceae.*—The fungal ancestors of the Verrucariaceae are doubtless derived from the Sphaeriaceae. Whether *Endocarpon* is represented by the same fungal ancestor as *Verrucaria* or not, will perhaps always remain undecided, but the probabilities are that such is the case. The apothecial and spore characters are essentially the same in both genera. The Sphaeriaceae form a group of the Pyrenomycetes as contrasted with the other families which belong to the Discomycetes.

III. THE ALGAL TYPES.

Concerning the algal ancestors of lichens, there is comparatively little difficulty to be encountered, for in the majority of species the life-history of the algal symbiont is known. We will consider only the forms of algae occurring in the Ascolichenes.

There is considerable confusion caused in the study of the lichen-algae by the fact that a given lichen-species is not absolutely limited to one and the same algal form. This is evident from the varying reports of lichenologists; for example, one author gives *Gloeocapsa* as the symbiotic alga of *Lichina confinis*, another gives *Polycoccus punctiformis*, a third gives both forms as occurring in this lichen. The latter author is perhaps right; that is, both species of algae occur in the same thallus. It may, however, be probable that one alga predominates, or even wholly supplants the other; in the specimens which came under my observation *Gloeocapsa* predominated. *Cystococcus humicola* is said to be the symbiotic alga of *Baeomyces roseus*, but I have found that *Gloeocapsa polydermatica* is also present. Some lichens have two forms of algae quite constantly present, as, for example, *Solorina crocea*. In spite of the variation and exceptions mentioned, the rule is that a given lichen contains only one species of alga and this is constantly present. We shall now briefly discuss the algal species which enter into the formation of the Ascolichenes.

1. *Cystococcus humicola.*—This species occurs in the majority of lichens (*Physcia*, *Parmelia*, *Usnea*, *Bryopogon*, *Cladonia*,

Evernia, etc.). It is a single-celled, spherical alga, and its only mode of reproduction while in the symbiotic association is by direct division; it has been successfully cultivated in culture media, independent of its fungal associate, and differs from the free form in being considerably larger. It varies, however, in size in different lichen-species; the nucleus is usually quite distinct in fresh material; the cell-wall is about normal in thickness and sometimes penetrated by the haustoria. In old herbarium material the algae become pale-green. As far as I have been able to observe, this alga is never associated with any other symbiotic alga within the thallus.

2. *Chroolepus* (*Trentopohlia*) *umbrina*.—This alga occurs quite uniformly in the Graphidaceae and the lower Verrucariaceae. It consists of sparingly branching filaments of loosely united cells; the individual cells are irregular in form, bright green, and contain irregular oleagenous granules of a reddish brown color, whose origin and function is unknown. In the free state these algae occur quite commonly on bark, rocks, soil, etc., in places somewhat shaded and moist. New cells are formed by division, in the majority of cases, at right angles to the filament; less frequently longitudinally.

The cells of the algae are enclosed by haustoria, but in no case have I been able to observe the penetration of the algal wall.

3. *Pleurococcus vulgaris* Menegh.—This species occurs in *Dermatocarpon*, *Acarospora* and in *Endocarpon*. It is single-celled, more or less irregular in outline and much larger than the free form, bright green with a bluish tinge while in the fresh state, and is quite common upon bark, rock, old fences, etc.

4. *Dactylococcus infusionum*.—The cells of this alga are elliptical and rather small; they usually are united in colonies of eight or twelve, sometimes fewer, and occur in *Nephroma*, *Solorina* and *Psoroma*.

5. *Nostoc commune* (*Nostoc lichenoides*).—This alga occurs in the family Collemaceae (excepting *Hydrothyria*). Whether it is *Nostoc commune* or not may be questioned. It is in all essential characters like the *Nostoc* occurring in the root-tubercles of *Cycas revoluta* and an ordinary *Nostoc* of our ponds and fresh-water lakes; the chains are always imbedded in a thick layer of gelatine or mucilage, through which the hyphae of the thallus ramify without forming haustoria about the algal cells. In size and development it differs but little from the free form of *Nostoc commune*, in the

majority of instances the individual cells being, perhaps, a little larger. The heterocysts, though well developed, are comparatively few in number. This alga has also been cultivated in culture-media independently of the fungal symbiont.

6. *Rivularia nitida*.—This alga occurs in *Polychidium*, *Omphalaria*, *Lichina*, etc. Like *Nostoc* it occurs in chains enclosed by a gelatinous layer through which the hyphae pass; its cells are quite irregular in outline, much more so than in the free form; heterocysts are wanting.

7. *Polycoccus punctiformis*.—This alga occurs in *Peltigera*, *Pannaria*, and *Stictina*. The cells are elliptical and imbedded in a gelatinous substance, sometimes in colonies of four or more. They are somewhat larger than the free forms which occur quite frequently upon trees, fences and upon lichen-thalli.

8. *Gloeocapsa polydermatica*.—I have found this alga quite constantly in *Baeomyces roseus* and in *Omphalaria umbella* as already indicated. The individual cells are spherical, with a thick gelatinous layer, and occur quite frequently in colonies of four or more. I have been unable to detect any difference between this and the free form. It is questionable whether it occurs constantly in *Baeomyces*. In *Omphalaria* it is associated with *Nostoc*.

9. *Sirosiphon pulvinatus*.—This alga, represented in *Ephebe pubescens*, is very much like the normal form in its growth and mode of branching. It grows from an apical cell which cuts off new cells in both planes forming branches of two or more cell-rows. This species also enters into the formation of the cephalodia of *Stereocaulon*.

For further detailed description and comparative study of the lichen-algae, the student is referred to any standard work treating of fresh-water algae. In making such comparisons, it is well to remember that the algae of lichens are, as a rule, larger and more irregular in form than the corresponding free algae. In the majority of lichens the algal species can not be absolutely determined. It is perfectly natural that the algae, as well as the fungal portion, should have undergone considerable structural as well as functional changes since their symbiotic association.

Plate 5 will aid in showing the relation of lichens to algae and fungi, that is their polyphyletic origin, but no attempt is made to indicate the polyphyletic origin of the fungal groups. The diagram also shows the relative position of the lichen-families in the scale of development.

PART II.

THE CLASSIFICATION AND SPECIAL MORPHOLOGY OF LICHENS.

CHAPTER I.

A SYSTEM OF CLASSIFICATION.

I. INTRODUCTORY CONSIDERATIONS.

The student on beginning a consideration of the classification of lichens is apt to adopt some one system with the impression that it is something fixed and definite, and this impression is likely to be strengthened on reading the laboriously worded descriptions of species. Nothing is, however, further from the truth.

There is at present no satisfactory natural or artificial system of lichens. All arrangements must of necessity undergo various changes as our knowledge of the life-history of the individuals becomes more and more perfect. This, however, does not imply that the systems proposed are without value. Any system is useful and in a sense indispensable in so far as it is in harmony with our actual knowledge of the subject under consideration. A system should therefore correspond as nearly as possible with the conceptions of the leading investigators on the subject. In a certain sense artificial system and natural system are only relative terms; as our scientific knowledge of a subject increases the corresponding system becomes more and more "natural," from which we may safely conclude that an absolutely natural system is practically and theoretically impossible since our knowledge of any subject is far from ultimate and is continually subject to change. It is, however, possible to set up useful systems which are quite "artificial," that is in which only a comparatively few of the known data are employed, but such systems are always much inferior to the "natural" system.

In the arrangement of lichens here proposed the endeavor has been made to conform to the results obtained by the ablest students of

the last quarter of a century, or since the time of Schwendener's epoch-making investigations. All older systems are wholly inadequate in the light of modern lichenology and for that reason must be discarded.

As already indicated (see Individualism) lichens form a distinct class of plants having a polyphyletic origin (see Polyphyletic Origin of Lichens). The question now arises, what subdivisions shall be made of this class? After careful consideration it was found that an arrangement into orders, families, genera and species without further subdivision was most natural and useful. We shall now discuss the characters selected for limiting these groups.

Order Characters.—The chief character to be considered in establishing orders is the method of spore-formation. All the known lichens can according to this be arranged in three orders, Ascolichenes, Basidiolichenes and Gasterolichenes. In the order first mentioned the spores are formed in spore-sacs by a process of free cell-formation; in the second, the spores are formed exogenously by the abstriction of the ends of specialized hyphæ; in the Gasterolichenes the spores are formed exogenously on basidia within specialized cavities. Only Ascolichenes occur in our territory. It may also be mentioned that the Basidiolichenes[1] are southern and that the existence of Gasterolichenes[2] is questioned by some authors.

The following are some of the groupings adopted by various lichenologists and which are still in use but which are unscientific and therefore untenable. Such are the groupings into homoeomerous and heteromerous; into gelatinous and nongelatinous; into crustaceous, foliose and fruticose; according to the nature of the algae (gonidia), into Archilichenes, Sclerolichenes, Phycolichenes, Gloeolichenes, Byssolichenes and Nematolichenes; into Pyrenolichenes and Discolichenes. These and other subdivisions which have the significance of orders or sub-orders are not to be recommended, because they add to the existing confusion. It would be impracticable

[1] The following authors have thoroughly discussed the Basidiolichenes:

Mattirolo, O. Contribuzioni allo studio del genera *Cora* Fr. Nuovo Giornale Botanico Italiano, **13**: 245–267. 1881.

Johow, P. Die Gruppe der Hymenolichenen. Jahrb. wiss. Bot. **15**: 361–409. 1884.

[2] The Gasterolichenes are discussed by the following authors:

Berkeley, J. M. Introduction to Cryptogamic Botany, 340. London, 1857.

Massee, G. On Gasterolichenes, a new Type of the Group Lichens. Trans. Royal Soc. London, **178**: 305–309. 1887.

in a work of this kind to enter into a discussion of the various systems and to explain their deficiencies. The student is advised to consult the various works in which the classifications mentioned are employed.

Family Characters.—In making the next comprehensive subdivisions of the order ascolichenes there are several important characters to be considered; such as the probable fungal ancestors, the structure and development of the apothecia and of the thallus. It must be admitted that the limitations of the families is as yet very unsatisfactory; this is in a great measure due to our uncertainty in regard to the identity of the fungal ancestors. It is very probable that the number of lichen-families could be made to correspond to the groups of fungi from which the fungal ancestors were derived. Although the development and structure of the apothecia are of great importance in defining the families there are other less important characters. For example, in the family Physciaceae the spores and in the Collemaceae the algae. The variable exceptions simply indicate that the present family limitations are far from reliable.

Generic Characters.—Theoretically, there are at least as many genera as there are natural series derived from distinct prototypes. This probability is especially applicable to the lower and smaller series, that is, those natural groups in which the phylogenetic processes have produced only comparatively slight changes. In the larger and biologically (therefore, also, morphologically) more complex series it is found convenient to recognize several or many genera, and such genera may even be distributed into different families. It is highly probable that *Lecidea*, *Biatora* (Lecideaceae) and *Parmelia* (Parmeliaceae) belong to the same series phylogenetically derived from a single prototype. The fact that they are not included in the same family is in part due to the uncertainty of their relationship and in part because an arrangement under separate families was found most convenient.

The spore-characters are of prime importance in delimiting genera. Constantly colored and colorless spores are not to be included in the same genus, but it must be remembered that all spores are colorless in the early stages of development. The number and direction of the septa are of great importance; in the majority of spores the septa are formed in two planes, that is, either only at right angles to the longitudinal axis of the spores or also in the longi-

tudinal plane; they are rarely formed diagonally to the longitudinal axis (Collemaceae, *Omphalaria*). Simple and septate spores are not usually included in the same genus. Septate spores again form genera according to the number and direction of the septa. The form of the spores also determines genera; for instance acicular and elliptical spores should not be included in the same genus (ex. *Biatora* and *Bacidia*). The number of spores in each spore-sac may determine genera, as in *Acarospora* and *Lecanora*; very rarely also the size of the spores and the structure of the spore-wall.

It must, however, be remembered that there are exceptions to any rule. Colored and colorless spores may occur in the same genus; likewise simple and septate spores, etc. Nor must it be supposed that the spore-characters alone determine the genera. We must, in addition, consider the development of the thallus, the apothecium, the exciple, the color of the apothecial disk, the algae, and the color of the thallus. A number of genera are based upon algal differences (*Sticta* and *Stictina*, *Psoroma* and *Pannaria*, and others).

I have found no occasion to maintain subgenera. In the genus *Cladonia* it might prove convenient to form subgenera based upon the development of the podetia; such as those with comparatively simple podetia as in *C. cariosa*, those with cup-bearing podetia as in *C. verticillata* and those with much branched podetia as in *C. rangiferina*. Upon closer examination it will however be found that it is difficult to draw the dividing lines and for that reason the subdivisions have not been made.

Species Characters.—At the very outset it must be admitted that our knowledge of the life-history of the majority of lichen-individuals is not sufficiently perfect to enable us to give the limitations of the species. In other words no one has as yet made sufficiently reliable observations to determine the possible variation of the individual plant, and until this is accomplished it is in many cases impossible to satisfactorily define species, much less to establish varieties, sub-varieties, forms and sub-forms. It is, however, true that in the higher forms of lichens the limitations of the species are fairly well determined.

In general it may be stated that in the establishment of species all known characters must be considered more or less. It is necessary to enter into the consideration of the minute structure of the thallus,

the apothecia and the spores, and, incidentally, to consider the substratum upon which the plants grow, and their distribution, both horizontal and vertical.

II. CHEMICAL REACTIONS.

For some years the chemical behavior of lichens to certain reagents has been considered of great importance in delimiting species. After careful testing I have finally decided to abandon the use of these reagents since they are practically valueless for the purpose recommended. That there are marked chemical reactions cannot be denied, for example the blue iodine-reaction of the thecial wall of the majority of lichens. This reaction is, however, so general in its occurrence that it can not possibly be of any value in establishing species, and the coloration varies in different individuals of the same species or even in the same plant at different periods of development. The same may be said of the other reactions, as those with solutions of potassium hydrate and calcium hypochlorite. That these reactions should be unreliable is evident when we consider the life-history of lichens; different individuals of one and the same species may develop upon substrata of widely different chemical composition. These chemically different substances adhere to the lichens and some soluble constituents are also taken up by the fungal symbiont which accounts for the difference and unreliability of the chemical reactions. It has already been indicated that perhaps some of the chemical compounds detected in lichens are derived from the substrata by absorbtion and are not the results of metabolic (or catabolic) processes in the plant itself.

The advocates of the chemical reactions advise great care in selecting chemically pure reagents and caution against carelessness in cleaning slides, cover glasses, etc. They advise a carefulness which is not called for; it is known that a rock-lichen and a tree-lichen of the same species are exposed to different environments, no matter how careful the experimenter may be in the selection of reagents and in cleanliness there is a difference in the chemical composition of the two plants which will more than neutralize the carefulness of the investigator and manifest itself by a difference in reaction.

The blue reaction with solutions of iodine is sometimes also noticeable in the hyphal tissues outside of the spore-sacs and paraphyses;

it has frequently been observed in the medullary tissues of the apothecial stalks of *Gyrophora* and in the hypothecium of other lichens. The reaction is, however, by no means constant and can not be considered as of value in the determination of species.

With regard to the algae it may be stated that they react like normal free species; they seem to have undergone no marked chemical changes since their association with fungi to form lichens.

CHAPTER II.

DESCRIPTIONS OF THE FAMILIES AND GENERA OCCURRING IN THE NORTHEASTERN UNITED STATES.

INTRODUCTION.

An attempt has been made to make keys as convenient aids for the use of beginners in the study of the families and genera. Although they are supposed to indicate natural arrangements of the several groups it must be kept in mind that such an arrangement is as yet very unsatisfactory, especially as regards many of the lower genera.

The occurrence of exceptions and intermediate forms constitutes the great stumbling block in the preparation as well as the use of any key. This difficulty gradually diminishes as the student becomes more and more familiar with his subject. Since many of the higher lichens never produce apothecia it is evident that the divisions of the key based upon the apothecial characters can not be made use of in their determination. A superficial general knowledge of lichens will, however, enable the student to give such sterile forms their generic position. It is urgently advised to begin with the study of fertile forms and to omit the consideration of sterile ones until a fair understanding of the limitations of the genera has been obtained.

The student of lichenology is absolutely dependent upon the use of a good compound microscope; no key or description can be made which will make it possible to avoid the use of this aid. It is also necessary to make good hand-sections of the thallus (inclusive of substratum when possible) and apothecium; these sections can be most satisfactorily studied when mounted in water.

Before attempting to use keys the student is advised to study the descriptions of the families and genera. Since the descriptions are simply the expression of our knowledge of the subject, they are accordingly perfect or imperfect as the case may be.

It is necessary to call attention to the extreme variability of lichen-structures, not only in size but also in form and coloration. In the same species different sections will show that the variation in

the thickness of the thallus may amount to one-third, and the same may be said of the different tissue-layers. The variation in the size of the spores is also very great; sometimes also the variation in form. In consideration of these facts it does not seem justifiable to establish genera based upon the relative thickness of the cortical layers, as Schwendener has done. Since nearly all lichen-tissues are highly hygroscopic, the dimensions of the various elements will vary with the amount of moisture present. In order to make the factors as constant as possible during examination, it is advisable to have all sections in the same media; if different media are used it is necessary to make due allowance for the changes they produce in the tissues.

The histological characters are also somewhat variable, and this is especially true of the hypothecium. In one section (of the same plant) it may appear semicortical, in another hyphal and in a third it may be almost impossible to recognize any structure, depending largely upon the portion of the apothecium from which the sections are made, and also upon the age of the plant. In general, however, the various structures are constant in their morphological characteristics; that is, the various tissues, as upper cortical layer, algal layer, medullary layer, lower cortical layer, and thalloid exciple, of different individuals of the same species are constant in occurrence and structure, though variable in dimensions.

Coloration of the tissues is quite variable, especially in the thallus. This variation depends upon the substratum, the age of the plant, the amount of the moisture present, the thickness of the various tissue layers, etc. Most species soon lose their normal color when placed in the herbarium, but if not too old the specimen may be made to regain its original color by immersing in water. Though certain colors occur quite constantly, such as green, yellow (orange), light-grey, black, greenish-blue, it will be found impossible to make use of delicate shades and tints in the determination of species.

Key to the Families.

Symbiotic algae belonging to the *Chlorophyceae*.

Thalloid exciple wanting.

Stipes or podetia present.

Spore-sacs dissolving, setting free the immature spores; disk closed.... ..... I. **Caliciaceae.**

Spore-sacs not dissolving; disk open, convex.

II. **Cladoniaceae.**

Stipes or podetia wanting.
Apothecia cup-shaped, flattened or convex.
III. **Lecideaceae.**
Apothecia irregular, linear or stellate; thallus crustaceous, mostly hypophloeodal.....IV. **Graphidaceae.**
Thalloid exciple present, or apothecia immersed in the thallus.
Apothecia discoid, sessile, rarely immersed.
Plasmic masses of spores united; spores two-celled.
V. **Physciaceae.**
Plasmic masses not united.....VI. **Parmeliaceae.**
Apothecia closed, hypophloeodal or immersed in the thallus; paraphyses very slender or gelatinized...VII. **Verrucariaceae.**
Symbiotic algae belonging to the *Cyanophyceae*.[1]
Algae belonging to the genus *Nostoc*, except in *Hydrothyria*, thallus foliose, dark blue, thin.....VIII. **Collemaceae.**
Algae not belonging to *Nostoc*.....IX. **Pannariaceae.**

GENERAL DESCRIPTION OF PLATES.

In order to avoid unnecessary repetition there is here given a general description of the plates illustrating the lichen-genera of the territory. With a few exceptions each plate illustrates one genus. Plate 15 shows the spore-sacs, spores and paraphyses of low forms of lichens, the apothecial and thalloid characters of which are sufficiently well illustrated in the plates of related genera.

The sequence of the figures illustrating the different structures is the same in most of the plates, that is, beginning with the upper left hand corner the plant is shown natural size, sometimes followed by a figure of a plant or portion of a plant somewhat magnified (C. ocular and 1 in. obj.); next follow the figures illustrating the structure of the apothecium and thallus, the drawings being made from hand-sections mounted in water (C. ocular, $\frac{1}{6}$ obj. and camera lucida); the spore-sac and paraphyses as well as the spores and algae are more highly magnified (C. ocular, $\frac{1}{10}$ in., water-immersion, and camera lucida).

Coloration of the hyphal tissue is indicated by shading.

Family I. CALICIACEAE.

There is little doubt that this natural and distinct group contains the lowest lichen-types. In fact the majority of the genera have

[1] The following genera of the *Pannariaceae* have bright green algae: *Nephromium*, *Solorina*, *Sticta* and *Psoroma*.

been classed as fungi by different authors, notably by Rehm, who has included *Calicium*, *Coniocybe*, *Cyphelium*, *Sphinctrina*, and *Acolium* under his division Calicieae of the Ascomycetes.

There is one character which distinguishes this group from all others, and that is the peculiar manner in which the spores are enabled to escape from the spore-sacs. The wall of the spore-sac begins to gelatinize near the apex; finally the greater portion of the wall is dissolved, liberating the immature spores; the spores remain in the space between the thecium and exciple until they are mature; they increase in size, the loose unevenly thickened exosporium enlarges and becomes dark or blue-black; they take up the required food substances by absorption from the enclosing tissues and the gelatinous imbedding material consisting principally of the gelatinized spore-sacs. When the spores reach maturity the exciple or apothecial covering opens by an apical pore which varies greatly in size. Distribution of the spores is brought about by the wind either directly or by its action upon the slender stipes.

The symbiotic alga is *Cystococcus humicola* Näg. (except in *Coniocybe*); it differs somewhat from the same form occurring in the higher lichens in its smaller size and less intimate association with the haustorial branches of the hyphae.

The genetic series *Mycocalicium*, *Coniocybe*, *Calicium*, *Cyphelium*, and *Acolium* is perfect, but there is a wide gap between *Acolium* and *Sphaerophorus*, the intervening generic links not being represented in the territory. The limitations of genera and species of the lower types are very uncertain, and this is particularly true of the American forms. In general the lower representatives of the family are in need of careful study and revision.

Key to the Genera.

Apothecia borne on slender stipes; plants small.
- Thallus crustaceous, usually wanting; spores dark. 1. *Mycocalicium*.
- Thallus crustaceous, always present.
  - Spores simple, colorless. 2. *Coniocybe*.
  - Spores two-celled, dark. 3. *Calicium*.
  - Spores simple, dark. 4. *Cyphelium*.

Apothecia nearly sessile; thallus crustaceous. 5. *Acolium*.

Apothecia terminal on a large rigid branching fruticose thallus. 6. *Sphaerophorus*.

1. Mycocalicium Reinke, Jahrb. wiss. Bot. 28 : 74. 1895.

It is an undecided question whether the representatives of this group should be classified with lichens or with fungi. The thallus is either rudimentary or wholly wanting; as a rule only a few algae suspended in a mesh-work of hyphae occur at the base of the stipe, and it is often also difficult to decide whether the thallus is normally absent or whether it has become accidentally worn away. For the time being the genus *Mycocalicium* includes all distinctly stipitate Caliciaceae in which the thallus is wanting or very rudimentary. The general morphology of the stipe and apothecium is similar to that of *Calicium* (see Plate 7); the paraphyses are simple, or sparingly branched. In old plants the entire thecium may fall away, leaving the cup formed by the exciple and hypothecium (perithecium).

On examining the spores it becomes evident that this genus includes representatives taken from the genera *Cyphelium* and *Calicium*; they are in all cases dark in color and either simple or two-celled without any distinct exosporium; this seems to be evidence that it is not a natural group. A more scientific method would perhaps be to classify them either as fungi or to include them in the genera *Cyphelium* and *Calicium*.

All representatives of this group have been taken from the genus *Calicium* and it is yet undecided how many species occur in the territory. It no doubt includes *C. Curtisii* Tuck., *C. fuscipes* Tuck. and *C. lenticulare* (Hoffm.) Ach. and perhaps a few others.

As far as I have been able to observe, the *Mycocalicia* occur upon pine trees or upon old pine boards, also, quite frequently, upon decaying wood (usually pine); owing to their small size and scattered development they are rather difficult to find. Their range is rather uncertain; the specimens which I have examined are mostly eastern.

PLATE 15. Fig. 1.

Mycocalicium Curtisii (Tuck.)

Spore-sac, spores and paraphyses. For the general morphological characters of the genus see Plate 7.

2. Coniocybe Ach. Act. Holm. 283, 1816.

This genus is closely related to both *Mycocalicium* and *Calicium*. I have been unable to note any differences in the apothecial char-

acters. The excipular or epithecial covering ("veil") is supposed by some authors to be more permanent in *Coniocybe*. The important distinguishing features are to be found in the spores and the color of the stipes and apothecia; the color varies from almost white through yellowish-brown to reddish-brown; the apothecia are of about the same size and form as they are in *Mycocalicium*; the stipes are somewhat more rigid; the spores are simple and colorless.

As a rule the thallus is very indistinct, though it is usually present. In the European *C. furfuracea* the thallus is well developed and of a marked sulphur color; I have seen only a doubtful sterile form of this species from Iowa, but Russell reports it from New England. It is much rarer than *C. pallida*.

In general the anatomy of the genus corresponds to that of *Calicium*. In the thallus we find the following differences: the algae are *Chroolepus* instead of *Cystococcus*; the hyphae are more slender, more branched and very indistinctly septate; the algae are quite intimately enclosed by haustorial branches; the paraphyses are few in number, considerably branched and variable in length; the spores are simple, colorless or faintly yellowish, spherical, with a distinct irregular exosporium which is readily removed. The function and composition of the exosporium is still unknown; it perhaps forms a protection to the spores. The mature spores as well as the hyphae of the stipe and apothecium also contain on the outside a deposit of acid crystals whose function is to protect the plant against attacks of animals, particularly snails (Zukal). The thallus is typically crustaceous and, although quite rudimentary in *C. pallida*, may be divided in three zones or layers; the uppermost, consisting of much-branched hyphae, devoid of algae, but containing in its meshes the remnants of dead algae and algal cell-walls, forms the protective covering; the second layer (b) bearing the algae (*Chroolepus*) constitutes the assimilating tissue, and below this is another hyphal layer (c) corresponding to the medullary layer in higher lichens continuous with the rhizoidal hyphae (d). Further observations are necessary to determine whether *Chroolepus* is the constant algal symbiont.

The representatives of this genus occur upon the bark of trees in shaded places; less commonly on decaying wood. *C. pallida* occurs throughout the territory.

PLATE 6.

CONIOCYBE PALLIDA Fr.

1. Plants natural size upon a piece of bark.
2. A single plant magnified.
3. Section through the middle portion of the apothecium.
   a, thecium; b, hypothecium; c, hyphae of the stipe.
4. Vertical section of the thallus.
   a, upper protecting layer; b, algal layer; c, hyphal layer analogous to the medullary layer of higher lichens; d, rhizoidal hyphae.
5. Spore-sacs, spores and paraphyses.
   a and b, mature spore-sacs with immature spores; c, spores escaping from the dissolved spore-sac.
6. Spores.
   a, exosporium.
7. Algae (*Chroolepus*) and hyphae from algal layer.

3. CALICIUM Pers. Ust. Ann. 7:20. 1794.

The natural position of this genus is a little doubtful, it being uncertain as to whether it is higher or lower than *Cyphelium*. Judging from the species occurring in the United States, it would be difficult to decide. From the study of European material (Hepp's Flechten Europas), I have concluded to place *Cyphelium* as the higher, since its thallus reaches a higher development.

In the majority of representatives of this genus the general characters of the stipes and the apothecia correspond to those of *Mycocalicium*, they being dark in color, quite slender, bearing a single globose apothecium, but it is at once distinguishable by the dark two-celled spores. The thallus is also uniformly present, though it does not attain any great development in the territory. It is uniformly crustaceous and not areolate. The essential structural differences as compared with *Coniocybe* are shown in plates 6 and 7.

Like the representatives of the preceding genera the *Calicia* occur in shaded places, upon tree-trunks, decaying wood, fences, etc. The majority of the species reported from the United States occur in the territory. *C. hyperellum* is, however, very doubtful, at least in the fertile form. Further study will decide whether the form from Iowa is really a sterile *Coniocybe furfuracea* or *Calicium hyperellum*.

PLATE 7.

CALICIUM QUERCINUM Pers.

1. Plants natural size upon a section of bark.
2. Apothecium and portion of stipe magnified.
3. Section of apothecium.
   a, thecium; b, hypothecium; c, hyphal tissue continuous with the hyphae of the stipe.
4. Vertical section of thallus.
   a, upper protecting layer; b, algal layer; c, medullary layer; d, rhizoidal hyphae.
5. Dissolving spore-sac, spores and paraphyses.
6. Spores.
   a, immature; b, mature.

4. CYPHELIUM Ach. Vet. Ac. Handl. 1814: 215. 1814.

Some authors, including Tuckerman, combine this genus with *Calicium*, but the spore-characters are, however, so well marked that I have decided to maintain it. In general, the representatives of the genus indicate a higher development than is met with among the *Calicia*. In the higher forms the thallus is very distinct, becoming even faintly areolate in species in which the stipe is shortened (*C. sessile*). Sometimes this shortening of the stipe is more apparent than real, that is, it becomes partially hidden by the thallus as in the European *C. corallinum* in which the thallus is quite thick. The general anatomical characters of this genus are the same as in *Calicium quercinum* (see Plate 7).

The habitat and distribution of the *Cyphelia* are about the same as that of the *Calicia*. As far as I have been able to observe, they are perhaps more restricted to the eastern states. The number of species occurring in the territory will perhaps not exceed six or seven. As already stated, the lower forms of this genus have been included in the genus *Mycocalicium*. *Sphinctrina* proper has not come to my notice from the territory. *S. tubaeforme* Mass. and *S. Anglica* Nyl. are doubtless species of *Cyphelium*.

For the general morphology of this genus see Plate 8. For the spore-characters see Plate 15, Fig. 1.

5. ACOLIUM Ach. Lich. Univ. 232. 1810.

In many respects this genus is essentially different from the preceding. The stipe is very much shortened, especially in the only

species occurring in the territory (*A. tigillare*); in the western *A. tympanellum* this organ is longer, but still much shorter than in *Calicium*. In *A. tigillare* the stipe as well as the greater portion of the apothecium is enclosed by the thallus, producing a conical projection around each apothecium; the thallus is very distinct, crustaceous, uniformly spreading and minutely areolate; each areole bears one, rarely two or three apothecia; the apothecia are very numerous, the disk is open and considerably flattened, especially in *A. tympanellum*. The general characters of the anatomical structure of the apothecium and stipe are the same as in *Calcium*. The sub-hymenial hyphae are dark colored; the spores are two-celled and dark; the paraphyses are sparingly present and rarely branched; the spore-sacs soon dissolve, setting free the spores while they are yet quite small and nearly colorless; the basal portion of the spore-sacs is narrowed and wholly colorless, forming a sharp contrast to the dark hypothecial hyphae.

The thallus differs but slightly from that of *Calicium*. No cortical structure is present, and the lower hyphal layer as well as the algal layer has increased in thickness indicating an increase in the assimilative function.

There is only one species reported from the territory, *Acolium tigillare*. Its natural substratum seems to be old pine fence boards, on which it occurs in large patches. From its position on fences in comparatively open countries it is evident that it has the ability to resist greater extremes of dryness than the majority of lichens. It seems to occur quite generally throughout the territory.

PLATE 8.

Acolium tigillare (Ach.) De Not.

1. Plants natural size upon a fragment of old fence-board.
2. Semi-diagramatic section of apothecium and thallus (magnified).
3. Section of apothecium.
   a, mature spores lying above the thecium; á, the bright colorless zone of the thecium formed by the narrowed basal portions of the spore-sacs; b, dark colored hypothecium.
4. Vertical section of thallus.
5. Spore-sac with immature spores and paraphyses.
6. Immature spores.
7. Mature spores.

6. Sphaerophorus Pers. Ust. Ann. 7: 23. 1794.

On studying *Sphaerophorus* as typified by *S. coralloides* we find some marked differences as compared with the foregoing genera. The stipe and primary thallus (see discussion of primary and secondary thalli, stipes and podetia in Cladoniaceae, p. 119) are wanting; the stipe is doubtless represented by the main stem and its branches, but it has become enormously elongated, branching dichotomously, and is entirely covered by the algal layer. The stipes in association with the symbiotic algae have become converted into a fruticose thallus; that is, we find the conditions to be closely analagous to those met with in *Cladonia* as will be seen upon a comparison of the two genera. In both the stipe or apothecial stalk has become converted into a fruticose thallus; in *Sphaerophorus* the assimilating surface is materially increased by the formation of numerous minute cylindrical branches; these secondary branches never bear apothecia; in some species (*S. fragilis*) the distinction between assimilating branches and apothecial branches is not so marked, and in these forms it is found that apothecia rarely or never occur, indicating that evolution is working toward the improvement of the assimilative function and neglecting the spore bearing function (see reproduction by spores, p. 90). The primary thallus has entirely disappeared, its function being supplanted by the secondary thallus.

The apothecial and spore-characters at once indicate the true position of this genus. As already indicated the globose apothecia occur at the ends of the main branches, each branch bearing one apothecium which is at first entirely enclosed by the thalline structure; the paraphyses are slender, simple and few in number; the spore-sacs have the same general structure as in *Acolium*, but the spores are simple with an enormously developed exosporium which becomes blue-black at the time of maturation; for some distance the hypothecial hyphal tissue (2, f) is dark, due to coloring substance deposited in the cell-walls.

The thallus (including main branches and secondary branches) possesses a typical radial structure. On the outside occurs a smooth brittle layer, consisting of hyphal cells usually extending vertically to the longitudinal axis. The cell-walls are so much gelatinized that it is almost impossible to recognize the outline of the individual cells. Internal to this layer occurs the algal layer consisting of a loose net-

work of hyphae in which the algae are suspended. The center is filled with rather loosely united hyphae extending in a longitudinal direction. The stem in cross-section presents the appearance of an effort having been made to increase the transverse diameter by separating the central elements, thus increasing the resistance to lateral tensions rather than to longitudinal which is doubtless what is required in a plant like *S. coralloides*.

Only a few species occur in the territory. They grow upon soil, more rarely upon rock; they are found in the North and in elevated areas in the East; very rarely in the tropics. With us the most common form is *S. coralloides* which is also the only species which is generally spore-bearing.

PLATE 9.

SPHAEROPHORUS CORALLOIDES Pers.

1. Portion of thallus natural size, showing the terminal globose apothecia (a).
2. Vertical section of apothecium (diagrammatic), magnified.
3. Section of apothecium.
   a, upper portion of thecium above which the free maturing spores lie; b, lower portion of thecium consisting of the narrowed spore-sacs; c and d, dark colored hypothecium.
4. Longitudinal section of a smaller thalloid branch.
5. Spore-sac with immature spores, and paraphysis.
6. Spores; a, immature; b, mature.

Family 2. CLADONIACEAE.

In general the representatives of this family indicate a much higher specialization than those hitherto described As far as the apothecia are concerned they indicate a closer relationship to the Lecideaceae than to the Caliciaceae; the disk is open and convex, the spore-sacs are not gelatinized as in the first family, the apothecia, without exception, are borne upon stipes or podetia, in which respect they show an undoubted analogy to Caliciaceae. It is, therefore, necessary at this point to indicate the essential differences between a stipe and a podetium, and also to discuss somewhat more fully the differences between primary and secondary thalli. From the standpoint of morphology the Cladoniaceae form, perhaps, the most interesting family.

a. Primary and Secondary Thallus.

The terms primary thallus and secondary thallus apply only to the genera *Pilophoron*, *Stereocaulon*, *Cladonia* and *Thamnolia*; they would not be applicable to *Baeomyces* any more than to the lower Caliciaceae.

The primary thallus is the thallus originally formed. It is crustaceous or warty in *Pilophoron* and *Stereocaulon* and foliose in *Cladonia*; in *Thamnolia* it is entirely wanting or at most rarely present. There is considerable chance for speculation as to the reason why the secondary thallus (podetium) should have supplanted the primary thallus; it is essentially a change from a horizontal thallus to a fruticose thallus. The prime factor which brought about this change was no doubt the presence of the apothecial stalk; this structure was suitable for the location of the assimilating algae, thereby forming a vertical thallus with a marked radial structure. Essentially the same conditions are met with in *Sphaerophorus* as already explained.

b. Stipes and Podetia.

According to definition stipes differ from podetia in being devoid of any symbiotic algae; both take their origin from the hyphal tissue of the thallus at a point somewhat below the algal layer; a group of hyphal branches form an apical area which extends upward pushing its way through the superimposed structures without inducing any increased cell-proliferation in them; the hyphae continue to grow upward parallel to each other, and very early in its development the apothecium begins to form at the apex. This is the mode of development of the stipes in the Caliciaceae as well as in *Baeomyces*. The so-called podetia of *Pilophoron* and *Stereocaulon* take their origin in a similar manner, but the algal zone takes part in the cell-proliferation covering the apothecium-bearing stalk; the algal layer of the stalk may not be entire, often being present only in patches.

The podetia reach their highest development in *Cladonia* and *Thamnolia*. In these genera we find that the podetium which was originally an apothecial stalk developed from the hyphal symbiont has become converted into a true lichen-thallus, replacing the primary thallus which has entirely disappeared in *Thamnolia* and some of the higher *Cladoniae*. Its primary function, which was that of forming a suitable support for the apothecia and aiding the distribution of

spores, has been partially (*Cladonia*) or wholly (*Thamnolia*) supplanted by a secondary function, that of assimilation.

The podetium, therefore, differs from the thalloid exciple, which is likewise a secondary adaptation for the purposes of assimilation, and is thus a thallus phylogenetically derived from an apothecial stalk (stipe). The thalloid exciple is likewise a thallus derived from the apothecium itself.

The algal symbiont of the Cladoniaceae is *Cystococcus humicola* Näg. (see *Baeomyces*). The exact fungal ancestors are unknown; but they are probably derived from the Patellariaceae (see Plate 5). The different genera are mainly derived from different fungal groups as is evident from the spore-characters. It is, however, very probable that *Thamnolia* and *Cladonia* are derived from the same fungal ancestor.

This family also illustrates very beautifully the degenerative tendency of apothecia and spores. *Baeomyces*, the lowest genus, is quite universally spore-bearing, likewise, *Pilophoron*; *Stereocaulon*, which is the third genus in the series, presents occasional sterile forms; the higher *Cladonias* are quite uniformly sterile, as for example *C. rangiferina*, *C. uncialis* and others, and *Thamnolia* never bears apothecia.

The species of this family are quite common and widely distributed; the soil is their more usual habitat though they also occur upon tree-trunks, old fences, and rocks.

Key to the Genera.

Thallus (primary) crustaceous or warty.
- Apothecia borne on thick stipes or nearly sessile. 1. *Baeomyces.*
- Apothecia borne on podetia (secondary thalli).
  - Podetia hollow; spores simple. 2. *Pilophoron.*
  - Podetia solid; spores four-celled. 3. *Stereocaulon.*

Thallus (primary) foliose or wanting; podetia hollow.
- Apothecia usually present; spores simple. 4. *Cladonia.*
- Apothecia always wanting: podetia simple, or sparingly branched, pointed. 5. *Thamnolia.*

1. Baeomyces Pers. Ust. Ann. 7: 19. 1794.[1]

The relationship of *Baeomyces* to the Cladoniaceae is based principally upon its apothecial characters. The generic characters

[1] According to O. Kuntze, the generic name *Tubercularia* Wigg., 1780, should be used instead of this.

are well marked and present some interesting features in lichenological development.

The thallus, as far as the representatives in our territory are concerned, is typically crustaceous, there being no trace of a cortical tissue. Even in the highly developed southern forms (*B. imbricatus*) in which the thallus has a distinctly foliose appearance, branched with ascending lobes, there is no cortical tissue proper, but simply a network of agglutinate hyphae with thickened gelatinous walls. The thallus usually covers a considerable area; it is of uniform thickness and adapts itself to the conformations of the substratum to which it is closely adherent; its color is usually bright green, becoming light colored on drying.

On examining vertical sections it is found that the algae extend nearly to the upper surface, there being only a thin upper layer consisting of the ends of hyphal branches mingled with the remnants of dead algae. The algal layer is well developed, followed below by a medullary tissue; the rhizoidal hyphae are rather deficient, and the hyphae throughout the thallus are slender; in the algal zone they are much branched, entirely enclosing the algal cells with numerous ectotrophic haustoria; the endotrophic haustoria are also very numerous and exceptionally distinct. The algae are probably *Cystococcus humicola* but differ from the usual forms by the presence of numerous pyrenoid bodies, usually two or three larger ones or many smaller ones in each cell; algal cells in all stages of division may be found. *Baeomyces* affords the best opportunity of studying the life-history of lichen-algae and their relation to the fungal symbiont. It need scarcely be mentioned that it is necessary to study fresh material. In some species (*B. roseus*, *B. aeruginosus*) a form of *Gloeocapsa* occurs in association with the normal algal form, below the *Cystococcus*, sometimes forming a layer of considerable extent. It is, however, not constantly present and should, therefore, be looked upon as a case of contingent symbiosis.

The apothecia are of medium size with either a flattened or convex disk and are borne upon thick simple stipes, which are sometimes so much reduced that the apothecia appear almost sessile (*B. aeruginosus*). These stipes may terminate in a single globose apothecium (*B. roscus*) or in several more or less agglutinate apothecia (*B. byssoides*). In the approximately sessile apothecia the disk is flattened; the epithecium and upper ends of the simple, rather

slender paraphyses are almost colorless or of a faint rosy tint to light-brown; the hypothecium is colorless. The central portion of the long stipes contains a very loose more or less reticulate hyphal tissue, while the outer portion consists of closely adnate hyphal cells extending longitudinally; the structure of these stipes, therefore, tends toward the hollow cylinder. The short stipes are more uniformly solid throughout; in color they are nearly white, thus forming quite a contrast to the thallus or the substratum.

The spores are spindle-shaped to almost acicular, colorless, simple or indistinctly two-celled or three-celled, usually bearing oil-globules, and the spore-wall as well as the septa are thin.

The *Baeomyces* are southern in their range, only about four species occurring in the territory; they usually grow upon sandy soil, rarely upon rocks and rotten logs.

PLATE 10.

BAEOMYCES ROSEUS Pers.

1. Plants natural size upon sandy soil.
2. Semidiagramatic section of apothecium, stipe and basal portion of thallus (magnified).
3. Apothecium and portion of stipe (magnified).
4. Section of apothecium.
5. Section of thallus.
   a, protecting covering; b, upper algal layer; c, hyphal tissue (conducting); d, lower algal layer; e, rhizoids.
6. Spore-sac with spores and paraphyses.
7. Spores; a, oil-globules; b, indistinct septum; c, simple spore.
8. *Cystococcus humicola (?)* undergoing division.
9. *Gloeocapsa polydermatica.*

2. PILOPHORON Tuck. Syn. Lich. 46. 1848.

Although it is not at all probable that *Pilophoron* is phylogenetically derived from *Baeomyces* its morphological characters are very similar, or at least present such resemblances which could readily be explained as evolutionary changes.

The horizontal thallus (primary thallus) is deficient, consisting of scattered crustaceous warts which are usually so small in size and few in number that they are entirely overlooked. In structure they resemble the podetial warts and will be discussed later. The podetia, which are neither more nor less than stipes covered by a thalloid

incrustation, are long, slender, simple or sparingly branched (usually once or twice toward the upper end), bearing terminal more or less globose apothecia, that is, it is the thallus instead of being spread over the substratum about the stipe has spread over the stipe itself, thus converting the originally mechanical structure into a physiological one as well.

Upon the examination of sections of the podetium it is found that the assimilating tissue is the outermost and consists of a network of hyphae in which the algae (*Cystococcus humicola*) are suspended; no cortical tissue proper is present. The algae are intimately associated with ectotrophic as well as endotrophic haustoria. This granular alga-bearing tissue forms a thin layer over the podetium extending to the base of the apothecia; it is only loosely attached to the internal mechanical tissue so that it is readily abraded, espe cially in the older specimens.

The mechanical tissue consists of a comparatively thick cylinder of closely adnate hyphae extending for the most part longitudinally. The interior is occupied by a very loose network of hyphae. The transition from the mechanical tissue proper to the central loose tissue is sudden and not gradual as in *Baeomyces*. From the above it is evident that we have here a typically radial structure built on the plan of a hollow cylinder.

The apothecia are of medium size, globose, the thecium lining the greater part of the surface; they appear as black terminal somewhat irregular knobs, somewhat thicker than the podetium. In structure they closely resemble those of *Baeomyces*; the hypothecium is black, and the epithecium and greater portion of the paraphyses are blue-black. This coloration is a marked contrast to the other groups of the family. The spores are oblong spindle-shaped, simple, colorless.

Only a few species occur in the territory; they are somewhat northern in their range and occur upon rocks in rather moist places.

PLATE 11.

PILOPHORON CEREOLUS (Ach.) Tuck.

1. Plants natural size.
2. Section of apothecium.
   a, thecium, b, dark hypothecium.
   c, beginning of colorless hyphae of the podetium.

3. Longitudinal radial section of thallus.
   a, thalloid wart; b, thin outer layer of hyphal network; c, inner mechanical tissue.
4. Spore-sac with spores and paraphysis.
5. Spores.
6. Algae.

3. Stereocaulon Schreb. Gen. Pl. 768. 1791.

The question whether this genus is phylogenetically derived from *Pilophoron* must for the time being remain undecided. It certainly indicates a close relationship, though considerably higher in the scale of development.

The primary thallus is practically wanting and we will therefore, limit our discussion to the podetium (secondary thallus); this is a typically fruticose structure, much branched, the branches being cylindrical, more or less twisted and otherwise contorted, thus forming quite a contrast to the podetium of the foregoing genus. The entire outer surface is covered by hyphal branches which in this genus form warty or branching isidioid outgrowths in association with the symbiotic algae. The alga-bearing tissue closely resembles that of *Pilophoron* though it is more highly developed structurally. No cortical tissue is, however, present. In regard to the algae the student will encounter difficulties; it will be found that a number of species are quite constantly present. They are a species resembling *Cystococcus humicola*, *Polycoccus punctiformis*, a species of *Scytonema*, *Sirosiphon pulvinatus*, besides other occasional forms. Naturally one is at a loss to know which is the alga peculiar to this group of lichens. After considerable study the conclusion was reached that a bright green alga closely resembling *Cystococcus humicola* is the form peculiar to *Stereocaulon*. It occurs by far the most frequently, while the others are instances of contingent symbiosis. The numerous hyphal projections from the outer surface of the podetium form a suitable structure to retain algae and soredia carried by the wind. I find that *Polycoccus punctiformis* is enclosed by a hyphal tissue foreign to *Stereocaulon* which is doubtless soredia of *Nephromium*, *Stictina* or some other group of lichens in which the symbiotic alga is *P. punctiformis*. *Sirosiphon* and *Scytonema* occur much less frequently. The algae which seem normal to *Stereocaulon* differ from the free *Cystococcus* in that the cells are quite irregular in form and size; they also have a tendency to arrange themselves in groups or even in chains; it may also be possible that they are a form of *Chroolepus*.

The great bulk of the podetium consists of hyphal cells extending for the most part in a longitudinal direction. The hyphae are less closely united than in the mechanical tissue of *Pilophoron*. There is no line of demarcation between the outer and inner portion, and the tissue becomes gradually less firm toward the interior. The center is, however, never hollow nor is the tissue as loose as in *Pilophoron*.

The apothecia are terminal, of medium size, somewhat globose, or distinctly flattened. The thecium and upper portion of the paraphyses is brown in color; the hypothecium is colorless and consists of a hyphal network with considerably gelatinized cell-walls; the depth of the thecium is quite variable; in *S. coralloides* the paraphyses and spore-sacs are very short. The spores are spindle-shaped or acicular, colorless, usually four-celled.

Stereocaulon is somewhat northern in its range. It also extends south in mountainous regions, occurring principally upon rocks.

PLATE 12.

STEREOCAULON CORALLOIDES Fr.

1. Part of plant natural size.
2. Portion of branch bearing apothecia.
3. Section of apothecium.
   a, thecium; b, hypothecium; c, gelatinous hyphal tissue.
4. Longitudinal radial section of thallus.
   a, portion of thalloid wart; b, external loose network of hyphae; c, inner mechanical tissue of longitudinal hyphae.
5. Spore-sac with spores and paraphyses.
   a, gelatinous portion of spore-sac.
6. Spores.
7. Algae.

4. CLADONIA Hoff. Deutsch. Flora Crypt. 114. 1795.

This is one of the largest groups of lichens and its study is fraught with considerable difficulty owing to the extreme variability in form associated with a great uniformity in the development of the tissue-elements.

The primary or horizontal thallus is usually foliose; in some of the lower forms it is crustaceous or warty, more or less lobed and ascending. Numerous thallus-lobes which retain a uniform size grow from the substratum and all ascend at about the same angle; owing to this uniformity in the size and form of the primary thallus it

plays little part in classification. Its structure is essentially as follows: There is an upper pseudo-cortical structure consisting of much branched hyphal cells extending vertically, the walls of which are so much gelatinized that it is impossible to observe the cell-outline; it is essentially a protective tissue though it also serves a mechanical function; below this is the algal layer, consisting of the algae (*Cystococcus humicola*) and a much-branched hyphal tissue, followed by a rather reduced medullary tissue; this is followed by a hyphal tissue in which the filaments extend in the direction of growth; there is no lower cortical layer.

The podetia or secondary thalli arise vertically from the upper surface of the primary thallus. It is the podetia which present the great diversity of form and which bear the apothecia. They vary from short and simple to much branched, nor is branching the only structural change, for the simple or nearly simple forms may vary greatly in size and structure, some being nearly smooth, while others bear numerous phyllodia or thalloid outgrowths structurally like the primary thallus and which are functionally comparable to the leaves of higher plants.

In the majority of *Cladoniae* the primary thallus finally disappears; even the basal portion of the podetia dies away while there is continual regeneration above. In some species the primary thallus perhaps no longer exists or at least has only a very temporary duration.

The podetia, no matter how variable their general conformation, are typically radial in structure, built on the plan of a hollow cylinder; their structure, as revealed by transverse and longitudinal sections, is as follows: There is an outer layer of tissue in all respects like the upper layer of the horizontal thallus, and this is succeeded by the algal layer in which the algae are quite deficient, which is followed by the medullary tissue; still more internally occur the longitudinal hyphal bundles which form almost a complete cylinder. The hollow central space is here and there traversed by hyphal bundles for the purpose of preventing collapse; mechanical adaptations are here highly developed.

The apothecia are terminal upon the podetia, or upon short apothecial stalks borne on the margin of the cup-shaped expansions of the podetia. They vary in size from medium to large, and are either simple or more or less agglutinate; the disk is convex; the epithe-

cium and upper ends of the simple paraphyses present two prevailing colors, brown and bright scarlet; in fact most authors separate the *Cladoniae* into two groups based on these color differences; the hypothecium is colorless, showing a marked cortical tendency.

The spores are simple, colorless, elliptical and of such uniformity in size and form that no specific distinctions can be based upon their characters. It must also be borne in mind that a number of species are quite constantly sterile, but in spite of this fact soredia are deficient. Special means of propagation and reproduction are not necessary, since the majority of *Cladoniae* are endowed with almost eternal life.

The *Cladoniae* are widely distributed, though some are typically northern; they occur upon the soil, old tree-trunks, old fences, and rocks.

PLATE 13.

Cladonia pyxidata Fr.

1. Plants natural size.
   a and c, sterile podetia; b, apothecia borne upon apothecial branches, e; d, horizontal (primary) thalli.
2. Diagramatic section of the cup of podetium showing the arrangement of the mechanical tissue (b).
3. Section of apothecium.
4. Vertical section of primary thallus.
5. Spore-sac with spores and paraphyses.
6. Spores.
7. Algae.
8. Portion of spermagonium.
   a, sterigmata bearing spermatia; b, hyphal network below the sterigmata continuous with the tissue (c) enclosing the entire spermagonium.
9. Spermatia.

(See also Plate 14.)

5. Thamnolia Ach.; Schaer. Lich. Helv. Spec. 44. 1823.

This genus is represented by only one species, *T. vermicularis*; which has probably been derived from some species of *Cladonia*.

The horizontal thallus is wanting. The vertical thallus is morphologically more highly developed than that of the *Cladoniae*, the outer layer, though thin, being for the most part cortical; the algal

layer is well developed; the internal mechanical tissue forms a continuous cylinder of considerable thickness. The diameter of the podetium is greater than in the majority of the *Cladonias*.

The podetium is either simple or sparingly branched. It is widest at the bottom, gradually tapering to a point, and presents a peculiar mealy appearance on its outer surface owing to a large deposit of acid crystals upon the cell-walls of the outer cortical layers. The color of the apothecia is a uniform greenish-grey.

Although several authors have reported apothecia and spores, it is now generally admitted that it is always sterile. After the most careful examination of European and American specimens I have been unable to detect the least traces of apothecia.

Thamnolia occurs upon soil and rocks in the higher altitudes and latitudes.

PLATE 14.

CLADONIA AND THAMNOLIA VERMICULARIS Ach.

1. *Thamnolia* natural size.
2. Longitudinal radial section of the podetium of *Thamnolia*.
   a, outer semicortical tissues; b, algal layer; c, inner hyphal tissue.
3. Young primary thalli of *Cladonia* on a section of old bark.
4. Portion of transverse section of the podetium of *Cladonia*.
   a, protective layer; b, algal layer; c, medullary layer; d, mechanical tissue of longitudinal hyphal bundles.
5. *Cladonia verticillata* Flk.
   a, apothecia upon short apothecial stalks; b, spermagonia.

Family 3. LECIDEACEAE.

At present the limitations of this family are uncertain, and this is particularly the case with the lower groups included in it. In general it may be stated that it is often doubtful whether a given genus should be placed with the Lecidiaceae, or with some other family. This doubt will continue until more reliable investigations are made in regard to the fungal as well as algal ancestors of the various groups; such investigations may lead to the establishment of a new family or families; the grouping here adopted is according to our present knowledge of the natural relationship of the genera.

The Lecideaceae differ from the two families preceding in the

absence of stipes and podetia; they are distinguished from the families following by the absence of the thalloid exciple.

There is little doubt that the generic groups of this family indicate a polyphyletic origin. We can, however, only state in general, that the several lichen-genera here included are doubtless derived from different fungal ancestors belonging to the Patellariaceae, a discomycetous group of the Ascomycetes (see plate 5). This is evident from the apothecial characters. There is also considerable confusion and uncertainty as to the algal symbionts of the lower groups; in the majority of species *Cystococcus humicola* Näg. forms the symbiont, but in some cases *Chroolepus umbrina*, or at least a related alga, takes its place. Some of the confusion is no doubt caused by the fact that the lower lichens are frequently capable of changing algal symbionts, as already explained elsewhere. *Bilimbia* seems to be quite constantly associated with *Chroolepus*, though I have examined undoubted representatives of this genus which were associated with *Cystococcus humicola*.

The following are the general characters of the family: The apothecia are sessile, from small to medium in size; disk convex or flattened, usually brown or dark in color; the spores vary greatly in size, form and in the number of septa; the thallus obtains its maximum development in *Gyrophora* and *Umbilicaria*, often reaching a diameter of several feet. In the lower forms the thallus is sometimes wanting or at least very rudimentary.

It is essential to call attention to the coloration of the various parts of the lichens belonging to this family. Generic distinctions are based upon the presence or absence of color in the hypothecium, as for example, *Lecidea* and *Biatora*, *Celidiopsis* and *Bilimbia*. Upon careful investigation it was found that such a distinction is unreliable, as all gradations from a black hypothecium (*Lecidea*) to a colorless hypothecium (*Biatora*) can be found. The color of the hypothecium as well as of the thallus, varies considerably with the nature of the substratum; for the time being, however, the distinctions based upon the color-differences of the hypothecium have been retained (see key). Some experiments on the color-variation in lichens are highly desirable.

Comparatively few of the Lecideaceae occur upon the soil; most of them grow upon bark; some occur upon mosses (*Bilimbia*); and a considerable number upon rocks (*Gyrophora* and *Umbilicaria*).

Key to the Genera.

Thallus indistinctly crustaceous to warty.
- Spore-sacs bearing about 16 simple colorless spores. 1. *Biatorella.*
- Spore-sacs bearing the usual number of spores (eight).
  - Hypothecium and spores colorless.
    - Spores two-celled. 2. *Biatorina.*
    - Spores simple. 3. *Biatora.*
    - Spores four-celled. 4. *Bilimbia*
    - Spores 6–8-celled, acicular. 5. *Bacidia.*
  - Hypothecium dark.
    - Spores simple, colorless. 6. *Lecidea.*
    - Spores four-celled, colorless. 7. *Celidiopsis.*
    - Spores four-celled, dark. 8. *Buellopsis.*
    - Spores two-celled, dark. 9. *Buellia.*
    - Spores two-celled, colorless. 10. *Catillaria.*
- Spore-sacs bearing from one to six spores; hypothecium colorless or yellowish.
  - Spores large, simple, colorless. 11. *Megalospora.*
  - Spores multilocular, dark. 12. *Lopadium.*
  - Spores multilocular, colorless. 13. *Gyalecta.*

Thallus foliose, entire.
- Spore-sacs bearing the usual number of simple, colorless spores.
  - Thallus small, 1 cm. in diameter, or less. 14. *Psora.*
  - Thallus very large, entire. 15. *Gyrophora.*
- Spore-sacs bearing one or two large multilocular spores; thallus very large. 16. *Umbilicaria.*

1. Biatorella De Not. Giorn. Bot. It. 2: 192. 1851.

Biatorella takes essentially the same position in this family that *Mycocalicium* does in the Caliciaceae. The thallus is quite constantly wanting, or only the simplest rudiment is present. The genus is characterized by the presence of sixteen spores in each spore-sac otherwise it closely resembles various lower genera of the family. As far as has been possible to observe, the spores are simple and colorless; in form they are sphaeroidal, having the general appearance of those of *Biatora*, though considerably smaller. The spore-sacs and paraphyses are very much as in *Biatora*. The hypothecium is dark, likewise the epithecium and upper ends of the paraphyses.

The genus is little known in the United States. Only one species (*B. geophana*) which grows upon sterile rocky or sandy soil, has

come to my notice. The apothecia being small, dark and scattered, makes it difficult for the collector to find specimens.

As with *Mycocalicium* it is questionable whether this genus should be included among lichens; some authors include *Biatorella* in *Biatora*.

PLATE 15, fig. 2.

BIATORELLA GEOPHANA (Nyl.).

Spore-sac with spores and paraphyses. For the general structure of apothecia and thallus see Plate 17.

2. BIATORINA Mass. Mem. Lich. 134. 1853.

The representatives of this genus are recognized by the two-celled, colorless, spindle-shaped spores. The thallus is rudimentary but readily recognizable; it is uniformly crustaceous, of a greenish color, and never becomes areolate or warty in any of the species examined. The algae are constantly *Chroolepus umbrina*. The much-branched chains consist of rather small cells in which the yellowish brown inclusions are quite distinct. The algal cells are closely entwined by the much-branched haustoria. In some cases the haustoria penetrate the algal wall (endotrophic haustoria). The hyphal cells are slender, much-branched and much-contorted.

The apothecia vary from small to very small, outline well-marked, somewhat cup-shaped; the hypothecium is colorless, and the epithecium yellowish to pale brown, which in connection with the spore-characters makes the recognition of the species easy.

According to some authors this genus should be included in *Gyalecta* from which it is, however, readily distinguished by the spore-characters as well as by those of the apothecium.

Its representatives, which seem to be few in the territory, occur upon soil and tree-trunks (*B. pineti*), more commonly upon the gametophytic generation of mosses, in which case the thallus is very deficient.

PLATE 16.

BIATORINA PINETI (Tuck.).

1. Plants normal size upon a piece of bark; a, apothecia.
2. Fragment of bark with plants magnified; a, mature apothecia; b, immature apothecia.

3. Section of apothecium.
   a, thecium; b and c, hypothecium; d, algal layer (often wanting); e, loose network of hyphae.
4. Section of thallus.
5. Paraphyses and spore-sac with spores.
6. Spores.
7. Algal chain; a, pyrenoid bodies.

3. Biatora Fr. Lich. Dian. Nov. 1817.

Authors have made this genus the dumping ground for all lichens which have the faintest macroscopical resemblance to the typical species. As a result the genus grew to such enormous proportions that it became impossible for a beginner in systematic lichenology to understand it at all. This I have endeavored to correct by isolating from *Biatora* the following genera: *Biatorella*, *Biatoridium*, *Biatorina*, *Bilimbia*, *Bacidea* and *Psora*, which simplifies the work of classification very materially and tends to prevent confusion, which is certainly desirable in our present arrangements.

The genus is characterized by a crustaceous thallus and simple colorless elliptical spores. The thallus, however, varies from typically crustaceous to warty and minutely foliose, merging into the foliose forms of *Psora*. I have, retained under *Biatora* all those forms in which the foliose character of the thallus is not sufficiently marked to be readily determined; in some species it is evident that the thallus varies from warty to faintly foliose and could, therefore, not be classed as foliose. *Biatora* is also liable to be confused with *Lecidea*, for we have the same spore-characters in both; the only difference is the dark hypothecium in the latter genus, but on careful examination it is, however, found that this character is not reliable, since we have a gradual series from colorless hypothecia in *Biatora* to dark hypothecia in *Lecidea*. The general characters of the thallus are the same in both genera; the algae are *Cystococcus humicola*.

The apothecia are of medium size, disk usually convex, sometimes flattened; the excipular margin is rarely somewhat elevated. The apothecia are also more or less immersed in the thallus, but not sufficiently to be characteristic; the color of the epithecium varies from light brown to dark and black.

Biatora is evidently closely related to *Parmelia*, as indicated by its apothecial and spore-characters. In general it may also be stated

that the thallus-characters of *Biatora* resemble *Parmelia* more nearly than those of *Psora*.

The representatives of this genus are widely distributed in the territory; they are most common upon the bark of trees; less common upon rocks and upon mosses. The limitations of the species are rather uncertain and there is considerable confusion in their systematic arrangement.

PLATE 17.

BIATORA VARIANS (Ach.) Tuck.

1. Plants natural size; a, clusters of apothecia.
2. A cluster of apothecia magnified.
3. Section of apothecium.
   a, thecium; b and c, hypothecium.
   d, algal layer.
4. Section of thallus.
5. Spore-sacs with spores and paraphyses.
6. Spores.

4. BILIMBIA De Not. Giorn. Bot. It. 2: 190. 1851.

The characters of this genus gradually merge into those of *Lecidiopsis*, the only essential difference being in the color, which is, however, not more marked than in *Biatora* and *Lecidea*. It is sincerely to be hoped that some investigator will take into consideration the significance of color-differences in lichens, especially in the lower forms; this would aid very materially in giving more definite limitations to the genera.

Only a few representatives of this genus have been observed within the territory. The thecium and hypothecium are colorless; the spores are spindle-shaped, colorless, usually four-celled, and the thallus is crustaceous, and to my knowledge never becomes foliose in character, which would place the genus below *Biatora*. I have, however, not attempted to follow out a strict phylogenetic relationship of the lower genera, since they are not sufficiently known.

The apothecia are of medium size, the disk is flattened or convex, and varies in color from yellowish brown to dark brown.

The algae are *Cystococcus humicola* and differ somewhat from the ordinary forms in being smaller and more united in colonies. They are intimately enclosed by haustorial branches, very frequently forming soredia, especially in *B. sphaeroides*. There is evidently an in-

timate organic association between hyphae and algae. The algae are also very numerous for such a lowly organized thallus.

The species occur on tree-trunks and mosses.

PLATE 15. fig. 4.

BILIMBIA FAGINEA Kbr.

Paraphyses and spore-sac with spores.

5. BACIDIA De Not. Giorn. Bot. It. **2**: 189. 1851.

The general characters of this genus resemble those of *Biatora*, but it is distinguished by the acicular colorless 4–10-septate spores, which are rather irregular in size and form, one end being usually pointed while the other is blunt and variable in diameter; they are also frequently curved and twisted.

The apothecia are of medium size, disk more or less convex to flattened and varying in color from light brown to black; the thecium is also more or less colored, usually yellowish brown; the hypothecium varies from dark brown to nearly black.

The thallus is typically crustaceous, sometimes becoming indistinctly areolate or coarsely granular with a grey or greenish color. As far as I have been able to observe, the algae are constantly *Cystococcus humicola*, and are intimately associated with the haustorial branches.

In several respects this genus presents degenerate characters. The paraphyses are granular; the spores are variable in size and form, as well as deficient in number and indistinct in outline. This, however, does not imply that this group presents any degenerative tendencies as lichens. The spores tend to degenerate because they are perhaps of little or no value in reproduction. Soredia are of frequent occurrence in this genus, in this respect resembling *Bilimbia*.

Quite a number of representatives of this genus occur in the eastern United States usually growing upon the bark of trees, rarely upon moss and rock. It is southern in its general range.

PLATE 18.

BACIDIA UMBELLA (Pers.) Mass.

1. Plants natural size.
2. Apothecium and portion of thallus magnified.
3. Section of apothecium.

4. Section of thallus.
   a, protecting layer; b, algal layer; c, medullary layer.
5. Paraphyses and spore-sac with spores.
6. Spores.

6. Lecidea Ach. Lich. Univ. 153. 1810.

As already stated in the discussion of *Biatora* this group presents the general characters of that genus. The following are some of the differences: It is somewhat lower in the scale of development, as is indicated by the more rudimentary thallus; the hypothecium is dark, though this is not a reliable distinguishing character, as already indicated; the thecium is also more or less brown to dark in color; the paraphyses are perhaps somewhat shorter and less distinct; the epithecium is quite constantly dark to black. In general, the tissue of the apothecium is somewhat more brittle.

The majority of the species occur upon rocks and tree trunks, a few upon old fences.

PLATE 19.

Lecidea melancheima Tuck.

1. Plants natural size.
2. A portion of above magnified.
3. Section of apothecium.
4. Section of thallus.
5. Paraphyses and spore-sac with spores.
6. Spores.
7. Algae.

7. Celidiopsis Mass. Flora, **15**: 487. 1857.

Further study of this genus is necessary to decide whether it should be combined with *Bilimbia* or not. It is distinguished from that genus by the dark hypothecium, a character which is by no means constant, even less so than in *Lecidea*. In all other respects it resembles *Bilimbia*, making, however, due allowance for varietal differences. Only a few species occur in the territory. Their habitat seems to be tree-trunks and moss.

PLATE 15. Fig. 4.

Celidiopsis.

Spore-sac, spores and paraphyses.

8. Buelliopsis.

I have separated this genus from *Buellia*, from which it is distinguished by the dark four-celled spores. It also differs somewhat in its apothecial characters. In *Buelliopsis* the apothecia are discoid, the margin is slightly elevated and somewhat irregular or wavy in outline. Only a few species have come to my notice. The thallus is crustaceous and comparatively rudimentary, consisting of a deficient network of hyphae with a few algae (*Cystococcus*), and does not enclose the apothecia as much as in *Buellia*; its color is grey to greenish. Further careful study of the genus is necessary in order to determine its limitations and position in the family.

In the early part of their development the spores are not constricted at the septa, but at maturity they become considerably constricted, much as in *Buellia*; they are rarely three-celled.

PLATE 15. fig. 5.

Buelliopsis vernicoma (Tuck.)

Paraphyses and spore-sac with spores.

9. Buellia De Not. Giorn. Bot. It. 2: 195. 1851.

In *Buellia* the apothecia are more or less immersed in the thallus which is thickly crustaceous and usually distinctly areolate; the spores are distinctly two-celled, dark, usually constricted in the middle. Reinke considers this genus closely related to *Rinodina*, which is true when superficially considered. In both genera the thallus is crustaceous and the apothecia are more or less immersed; the apothecia are also more or less irregular in outline, especially in *Buellia*, which also has a dark hypothecium, and the thecium is also frequently quite dark in color.

The thallus varies from grey, through greenish to more or less dark. (*Buellia* will be further considered under *Rinodina*.)

Most of the species occur upon rocks, more rarely upon bark and old fences.

PLATE 20.

Buellia parasema (Ach.) Fr.

1. Plants natural size.
2. Plants magnified.
3. Section of apothecium.

4. Section of thallus.
5. Paraphyses and spore-sac with spores.
6. Spores; b, of *B. parasema;* a, common form in other species.
7. Algae.

10. Catillaria Ach. Meth. Lich. 33. 1803.

In our territory *Catillaria* is represented by only one species, *C. grossa*. Like most of the lower Lecidiaceae, this genus requires further study. Tuckerman and others included it in the uncertain group *Heterothecium*. Its general characters remind one strongly of *Lecidea*; the hypothecium is dark blue to black, the thecium only faintly colored; the apothecia are of medium size, disk flattened, with slightly raised excipular margin; the epithecium and outer perithecium are black.

The thallus is quite rudimentary in structure, being very thin, smooth, somewhat scaly or paper-like; no cortical tissue is present. The hyphae of the thallus, as well as of the apothecium, are quite brittle and rather short-celled.

The algae occur in small groups and are doubtless *Pleurococcus vulgaris*. The individual algal cells are considerably smaller than those of *Endocarpon*, but otherwise similar.

The genus is easily recognized by the distinctly two-celled, colorless, rather large spores. The paraphyses are more slender and less uniform in length than in *Lecidea*. Only a few representatives of this genus are known. *C. grossa* occurs upon the bark of ash and perhaps other trees. Since so little is known concerning this species nothing definite can be stated concerning its range; it is, perhaps, eastern and northern.

PLATE 21.

Catillaria grossa (Pers.) Blomb.

1. Plants natural size.
2. Section of apothecium.
3. Section of thallus.
   a, dermal layer; b, algal layer; c, medullary layer.
4. Spore-sac and paraphyses.
5. Spores.
6. Algae showing the tendency to arrange themselves in chains.

11. Megalospora Meyen, Nov. Act. Acad. Leop. 19: 228. 1843.

In general appearance *Megalospora* closely resembles *Catillaria*. The apothecia are somewhat larger and disk more convex. The

thallus presents almost the same external appearance as to color and conformation, but the minute anatomy is somewhat different. The algae are *Cystococcus humicola*, very intimately associated with the haustoria, both ectotrophic and endotrophic; this union is so intimate that it is almost impossible to separate the symbionts without destroying the algae or the hyphae. The upper layer of the thallus contains the remnants of numerous dead algae whose contents have been absorbed by the haustoria. The algae are evidently soon exhausted by the absorbing haustoria, which necessitates the formation of new algal cells by division. The algal cells are quite variable in size, which seems to depend upon the intimacy of their union with the hyphae; if they are enclosed by few haustoria they may develop to considerable size before dividing.

As in *Catillaria*, the hypothecium is black or dark blue.[1] The entire thecium is likewise more or less blue-black. The spore-sacs contain one, rarely two, large simple spores. The two layers of the spore-wall are very distinct; the outer layer (exosporium) is quite thick and gelatinous, which enables the spore to adhere to any substratum when moist.

This genus, which is likewise separated from *Heterothecium*, is represented by a single species (*M. sanguinaria*). It is not very common, occurring upon tree trunks, and is readily recognized by the comparatively large convex apothecia upon the light grey thallus.

PLATES 22 AND 23.

MEGALOSPORA SANGUINARIA (L.) Kbr.

1. Plant natural size.
2. Section of apothecium.
3. Section of thallus.
   a, dermal layer; b, algal layer; c, medullary layer (compare with c of plate 21.
4. Spore-sac with spore and paraphyses.
5. Spores; a, gelatinous exosporium; b, endosporium.
6. Algae (a) and hyphae (b); c, pyrenoid bodies.

12. LOPADIUM Kbr. Syst. Lich. Germ. 210. 1855.

Some authors include this group of lichens in the conglomerate genus *Heterothecium*. It is represented by a few well-characterized species.

[1] European specimens are said to have a colorless hypothecium. Some authors recognize varieties based upon the "red" or "yellowish" color of this structure.

The thallus is crustaceous and quite uniformly spreading. There is no cortical tissue proper; the upper part of the thallus consists of a thin layer of agglutinate hyphae with much gelatinized cell-walls (protective covering). Below this is found the algal layer, consisting of the algae (*Chroolepus umbrina*) enclosed by a network of rather slender hyphae. The rhizoidal hyphae are quite numerous and extend into the substratum to a considerable depth. It must also be mentioned that groups of *Polycoccus punctiformis* frequently occur in different parts of the thallus and at the base of the apothecia (contingent symbiosis). Soredial patches (soralia) are frequently present.

The apothecia are of medium size, distinctly discoid and loosely sessile upon the thallus, to which they are attached by hyphal bundles. A reddish brown or a black coloration pervades nearly the entire apothecial structure. This coloration is principally due to a deposit in and upon the hyphal cell-walls of some lichen acid. The paraphyses are simple and quite distinct. The spores are multilocular and vary from colorless to brown and reddish brown.

The species are southern, occurring upon the bark of trees and on mosses.

PLATE 24.

LOPADIUM PEZIZOIDEUM (Ach.) Kbr.

1. Natural size; a, apothecia.
2. Section through the thallus and margin of the apothecium. a, thecium; b and c, hypothecium; d, excipular layer; e, hyphae connecting the apothecium with the thallus (f and g).
3. Section of thallus.
4. Paraphyses and spore-sac with spore.
5. Spores; a, earlier stage of development; b, mature spore.

13. GYALECTA Ach. Lich. Univ. 151. 1810.

This genus of lichens is so little understood that it is practically impossible to give its limitations, most of its representatives being included by authors in other lichen-genera. The following are the generic characters as far as they can be determined.

The thallus is crustaceous in the majority of species; in the higher forms it consists of minute foliose lobes with upper and lower cortical layers. In the majority of species it is usually quite dark, above and below. The algae are apparently *Cystococcus humicola* in all the species examined; incidentally *Polycoccus punctiformis*

and several other species of algae occur in and upon the thallus, especially in the lower forms. The apothecia are discoid, from minute to medium in size, with a flattened disk; the epithecium and upper ends of the simple paraphyses are dark; the hypothecium is non-cortical and usually colorless; the spores are quite large, multilocular, oblong-elliptical or nearly spindle-shaped and usually colorless. It is, however, probable that the hypothecium as well as the spores are dark colored in some species.

The *Gyalectas* are quite generally distributed; they occur upon rocks and trees.

PLATE 15. fig. 6.

GYALECTA.

Paraphyses and spore-sac with spores.

14. PSORA Hoffm. Flora Deutsch. Crypt. 161. 1795.

This is the first group of lichens belonging to the Lecideaceae in in which the thallus is typically foliose. The upper cortical tissue is comparatively thick and consists of two layers; the upper, which may be designated as the dermal, consists of hyphal cells lying horizontally, with enormously thickened gelatinous cell-walls and much reduced cell-lumina; the layer below this consists of nearly normal cortical cells extending vertically, differing from the normal ones in that their cell-walls are thicker (more gelatinous), while the cell-lumina are much reduced.

The algal layer consists of the alga *Cystococcus humicola* enclosed by a network of ordinary hyphae instead of typical haustoria so that the hyphal tissue has the semblance of being cortical. The medullary tissue consists of a comparatively close network of hyphae. There is no lower cortical tissue, but the terminal hyphal branches are perhaps somewhat more crowded and show a tendency to arrange themselves vertically to the surface.

The color of the thallus is quite variable; the upper surface may vary from light grey to black with the lower surface lighter; in some species the margin is almost white. In the dark thallus the lower surface is practically of the same color as the upper. The thallus-lobes may be somewhat ascending or closely adnate to the substratum.

The apothecia are small to medium, distributed over the thallus, but sometimes near the margin; they are usually disk-like but more

or less immersed in the thallus; sometimes almost entirely so (*P. Russellii*). The entire apothecial structure is more or less rusty colored; there is no thalloid exciple.

The spores are simple, elliptical, colorless, closely resembling those of *Biatora*.

The *Psoras* occur upon rock and soil and seem to be quite generally distributed; by many authors they are included in *Biatora*

PLATE 25.

PSORA RUSSELLII (Tuck.)

1. Plants natural size upon a piece of rock; a, apothecia; b, single thallus.
2. Thallus with apothecium, enlarged.
3. Section of apothecium.
4. Section of thallus.
   a, epidermal layer; b, dermal layer; c, algal layer; d, medullary layer; e, lower limiting layer.
5. Paraphyses and spore-sac.
6. Spores.

15. GYROPHORA Ach. Lich. Univ. 36. 1810.

The representatives of this genus form a remarkable group of lichens, both as to size and structural characteristics. Their relation to other genera is as yet not definitely determined; their life-history has not been sufficiently studied to warrant any reasonable conjectures as to their phylogenetic relationships.

The thallus, which is in all cases typically foliose, varies in size from medium to very large. The smaller thalli may either be single, or form a cluster, more or less imbricated. No matter what the size of the thallus may be, it is always entire, fastened to the substratum by the umbilicus. The margin is quite generally more or less torn and frayed out or somewhat incised, rarely also bearing thalloid branches or cilia. The prevailing colors of the upper surface are grey to black. The lower surface is usually black and presents various structural modifications, sometimes bearing black cilia (usually aërial), and there are generally special mechanical adaptations consisting of vertical as well as horizontal plates of cortical tissue for the purpose of supplying an adequate support to the large thallus. (See discussion of Mechanical Adaptations, p. 81.)

The following structures are revealed upon the examination of vertical sections: The upper cortical layer is comparatively thin and

shows some resemblance to the cortical tissue of *Psora* in that the cell-walls are much gelatinized and cell-lumina reduced; the uppermost cell-layers are dark colored, due to a deposit of coloring substance in and upon the cell-walls; the algal layer is quite deficient for so large a thallus and consists of the alga *Cystococcus humicola*, enclosed by haustoria; the medullary layer, which is quite normal in structure, is also very deficient; the lower cortical layer is, however, enormously developed, which is in distinct contrast to the majority of foliose lichens. The outermost layer of this tissue as well as of the mechanical plates is dark colored. The lower cortical layer is, however, not of uniform thickness, and in places may be quite thin. It is usually dotted with warty elevations.

The umbilicus is a short stem-like structure of cortical tissue supporting the thallus. From its base the long branching root-like rhizoids extend deep into the substratum; these are in all respects closely analogous to roots in the higher plants.

The apothecia are very peculiar in structure. Each apothecium, or apothecial group, consists of numerous short vertical, twice or thrice dichotomously branched apothecial stalks. The stalks themselves are miniature fruticose thalli, analogous to the podetia of *Cladonia*, growing from the upper surface of the thallus proper. Structurally they consist of a thin external gelatinous or semicortical, dark-colored hyphal tissue, the interior being occupied by a medullary tissue bearing a few algae. The apothecia proper are terminal on the stalks, and are very simple in structure, as will be seen from a study of the plate; no trace of a thalloid exciple is present.

The apothecial branches are so closely united that the apothecial patch has the appearance of a single apothecium with a convex convolute disk, adnate upon the thallus. The entire apothecial structure, inclusive of the stalks, appears black to the naked eye.

The spores are simple, elliptical, colorless; their plasmic contents are sometimes more dense at the middle, producing the semblance of a septum.

The *Gyrophoras* are northern in their range but are also quite common in the mountainous regions of the temperate and torrid zones. They occur principally upon rock and soil. The genus is usually united with *Umbilicaria*.

PLATE 26.

GYROPHORA MÜHLENBERGII (Tuck.)

1. Portion of thallus natural size; a, apothecial groups; b, umbilicus.

2 and 3. Section through apothecia, apothecial branches and thallus. a, thecium; b, hypothecium; c, medullary tissue with algae; d, semi-cortical covering.

3. a, colored portion of cortical layer; b, colorless portion; c, spermagonium; d, algal layer; e, medullary layer; f, lower cortical layer; g, algal colonies (*Microcystis*).

4. Paraphyses and spore-sac.

5. Spores; b, indistinct septa.

6. Algae; b, pyrenoid bodies.

7. Colony of *Microcystis;* c, outer covering.

7′. Optical section of 7.

8. a, Sterigmatum with spermatia; b, spermatia much enlarged.

16. Umbilicaria Hoffm. Fl. Deutsch. Crypt. 109. 1795.

The general appearance and structure of the thallus of *Umbilicaria* resembles that of *Gyrophora*. The following are the differences: Cilia, rhizoids and mechanical plates are wanting; the numerous caps with basal rings of hyphal tissue (pustules) assist in forming the necessary mechanical support. The histology and coloration is much as in *Gyrophora*.

The apothecial patches usually differ considerably from those of *Gyrophora*, being smaller and consist of clusters of minute cup-shaped apothecia; instead of being sessile upon the cortical layer of the thallus, this tissue enters into their formation. The individual apothecia are, however, not all cup-shaped; they may become elongated, curved or convolute.

The arrangement of the individual apothecia relative to each other produces a peculiar appearance of the upper surface of the apothecial patch, resembling very closely the outline of the dentine in the molar of a ruminant (also the case in *Gyrophora*). The entire apothecial tissue is more or less dark colored.

The spores are large, multilocular, brown in color; each spore-sac contains only one.

The range and habitat of this group is much as in the preceding; they are perhaps less northern. It is represented in the territory by about four or five species.

Sirosiphon pulvinatus and a form of *Microcystis* occur quite frequently upon both upper and lower surfaces of the thallus of *Gyrophora* as well as *Umbilicaria*, and more constantly between the apothecial stalks. This is evidently a case of contingent symbiosis.

PLATE 27.

UMBILICARIA PUSTULATA (L.) Hoffm.

1. Portion of thallus natural size; a, apothecia; b, pustules.
2 and 3. Section through apothecial branch and thallus.
4. Paraphysis and apothecium with immature spore.
5. Spores; a, spore before the formation of septa has begun; b, later stage; c, mature spore.
6. Algae and enclosing hyphae (haustoria).

Family 4. GRAPHIDACEAE.

There is little difficulty in recognizing the limitations of this family; but at first it will seem doubtful as to the position it should be given in the sequence of families; judging from the representatives occurring in our territory it would seem that this formed the lowest family in the series. But if we include *Rocella* it at once receives a high position in the series. For a long time I was in doubt as to the true position of this genus, but finally came to the same conclusion as Reinke and consider it as a lecideine type, as is indicated by its apothecial characters. There are, however, some serious objections to such a conclusion. First, as to the dark hypothecium of *Rocella*, it may be stated that this does not indicate an unmistakable lecideine type, since we have a number of genera among the Lecideaceae with colorless hypothecia; furthermore *Pyxine* is recognized by its dark hypothecium, though it evidently does not belong to the family. Another objection to placing *Rocella* with the Graphidaceae is the form of the apothecia; they are typically discoid and not irregular or linear; it must, however, be admitted that the most suitable position at present is among the Graphidaceae and it is this consideration which determines the position of the family here adopted.

The representatives of the family, as far as they occur in the territory, are characterized as follows: The thallus is crustaceous, very rudimentary, and for the most part hypophloeodal; the symbiotic algae are mostly *Chroolepus*.

The generic groups indicate a polyphyletic origin, but it can only be stated in a general way that the ancestral forms of the fungal symbionts are derived from the Phacidiaceae (plate 5), as is evident from the apothecial, as well as the spore-characters; the fungal ancestor of *Graphis* was doubtless derived from the genus *Hysterium*.

The genera representing this family are southern in their distribution, though some species are very common throughout the territory, as for example *Graphis scripta*. They generally occur upon the smooth bark of trees. Some of the southern species reach a high development in the thickness of the thallus, though the structure remains quite simple.

KEY TO THE GENERA.

Spores 2–8-celled, or simple.	
Spores 2-celled, colorless.	1. *Hazslinskya.*
Spores 4–6-celled, acicular, colorless.	2. *Opegrapha.*
Spores 8-celled, large, oblong, colorless.	3. *Graphis.*
Spores simple, colorless.	4. *Xylographa.*
Spores 4-celled, not acicular.	5. *Arthonia.*
Spores multilocular.	
Spores constricted in the middle.	6. *Mycoporum.*
Spores not constricted, colorless.	7. *Arthothelium.*

1. HAZSLINSZKYA Kbr. Parerga Lich. 257. 1865.

This is another doubtful and lowly organized genus of lichens represented by only a few species which have been found in Europe as well as the United States; the American forms or form have been included under *Opegrapha* as *O. demissa*.

The thallus as well as the apothecia begin their development below the surface of the substratum; after a time the thallus forms a thin whitish film over the substratum; it never forms more than a mere network of hyphae in which clusters of algae are suspended (*Cystococcus humicola* and perhaps *Pleurococcus vulgaris*). There is no differentiation into layers; the rhizoidal hyphae extend into the substratum to a considerable depth.

The apothecia soon break through the thin layer of the superimposed substratum and appear as minute black dots; upon examination with a lens they appear more or less orbicular or somewhat elongated with irregular outline; the disk is flattened. The epithecium and upper ends of the simple more or less granular paraphyses are dark in color. The hypothecium (perithecium) consists of a close network of more or less brownish hyphae.

The spores are colorless, of medium size and distinctly two-celled, one cell being larger than the other, constricted at the septum; the spore-wall and septa are thin.

As far as known the species occur upon trees in the north temperate zone.

PLATE 15. fig. 7.

HAZSLINSZKYA DEMISSA (Tuck.)

Paraphyses with spore-sac and spores.

2. OPEGRAPHA Humb. Fl. Friberg, 57. 1793.

The thallus is rudimentary and for the most part hypophloeodal, finally forming a thin film over the substratum. Structurally it is almost as simple as in *Hazslinszkya*, consisting of a much branched network of slender hyphae in which the chains of algae (*Chroolepus umbrina*) are suspended. Numerous haustorial branches enclose the algal cells; endotrophic haustoria also occur.

The apothecia are usually numerous, small, linear, more or less curved, projecting somewhat above the surface of the substratum. The hypothecium (perithecium) and epithecium are black. The paraphyses are usually branched, granular and more or less gelatinized.

The spores are colorless, spindle-shaped to almost acicular, usually four-celled.

The *Opegraphae* range from the south to the north temperate zones. The majority of the American species occur in the East. They live principally upon trees, rarely upon rock, and are sometimes parasitic upon other lichens.

PLATE 28.

OPEGRAPHA VARIA Pers.

1. Plant natural size.
2. A small portion magnified.
2'. Vertical (transverse) section through apothecium, thallus and subsubstratum (semidiagramatic).
3. Section of apothecium.
4. Section of thallus.
5. Paraphyses and spore-sac.
6. Spores.
7. Algae and hyphae.

3. GRAPHIS Ach. Lich. Univ. 46. 1810.

The species of *Graphis* in so far as they occur in the territory are simple in structure, and in all but spore-characters they closely resemble the *Opegraphas*. The thallus is partly hypophloeodal finally forming a thin film over the substratum. The algae (*Chroo-*

lepus umbrina) are enclosed by a network of hyphae. In the tropical representatives of this genus the thallus becomes greatly thickened but never reaches beyond the crustaceous stage.

The apothecia are markedly linear, variously curved and branched, extending somewhat above the substratum and thallus. The hypothecium (perithecium) and epithecium are dark colored in the majority of species; but in many of the southern forms the epithecium and thallus are white. The paraphyses are somewhat longer than in *Opegrapha* and quite granular.

The spores are comparatively large, six to twelve-celled, colorless, somewhat curved; the exosporium is frequently wavy in outline. In *G. elegans* spores are quite constantly wanting; it is perhaps a sterile form of *G. scripta*.

The species are distinctly southern in their range, only a few occurring in northeastern America. They occur upon the bark of trees, preferably on smoother barks.

PLATE 29.

GRAPHIS SCRIPTA Ach.

1. Natural size.
2. Portion magnified; a, apothecium.
3. Section of apothecium: b and c, colorless and colored portions of hypothecium.
4. Section of thallus.
5. Paraphyses and spore-sac.
6. Spores.

4. XYLOGRAPHA Fr. Syst. Mycol. 2: 197. 1823.

This genus is represented by only a few species. It should perhaps be placed before *Graphis*, as it is evidently lower in the scale of development than that genus, but as far as the representatives of these genera occur in the territory *Xylographa* reaches the greater perfection. Its present systematic position will no doubt be changed when the plants are more critically studied.

The thallus begins its development below the substratum but finally spreads over the surface, forming a thin, white layer. The algae (*Cystococcus humicola*) occur in clusters enclosed by the hyphal network. The hyphae intermingled with the remnants of dead algae and even fragments of the substratum form a protective layer above the algae. The rhizoidal hyphae are numerous and extend far into the wood on which they grow.

The apothecia are linear or irregular, extending parallel with the fibres of the substratum; their outline is not as clearly defined as in *Graphis*, they being more or less covered by the thallus and substratum. The upper ends of the indistinct simple paraphyses are dark colored, likewise the epithecium. The hypothecium is nearly colorless. The spores are rather small, elliptical, simple, colorless, and usually sparingly produced.

The species occur upon rotten logs in the north temperate zone.

PLATE 30.

Xylographa paralella Fr.

1. Natural size.
2. Portion magnified.
3. Section of apothecium.
   a, thecium; b, hypothecium; c, hypophloeodal hyphal tissue.
4. Section of thallus.
5. Paraphyses and spore-sac.
6. Spores.
7. Algae (*Cystococcus humicola*).

5. Arthonia Ach. Lich. Univ. 25. 1810.

This is one of the most difficult groups of lichens for several reasons. It contains a large number of species, although only comparatively few occur within the territory. With few exceptions the genus presents no marked characters; spores are very frequently wanting, and the thallus is in all cases deficient and variable in its algal characters. Only a critical study of good material will enable the student to make an approximate identification of species.

The thallus begins its development below the substratum; in fact it remains partly hypophloeodal in the majority of species. In the higher species the thallus becomes distinctly crustaceous, even somewhat areolate; no cortical tissue is ever present. Perhaps the most remarkable feature about the entire group is the algal tissue. The algae are numerous and almost entirely enclosed by ectotrophic haustoria, and endotrophic haustoria are also common. In no group of lichens is the structural relationship between fungus and alga so intimate, and this is true whether the alga is *Cystococcus humicola* or *Chroolepus umbrina*. Incidentally it may be remarked that since both forms of algae are represented it is evident that the genus might be subdivided according to these algal differences.

The characters of the apothecia are also very variable. As in the preceding groups these begin their development below the substratum; some time before maturity they break through the surface; very rarely they remain covered over by a thin layer of the thallus and remnants of the substratum; they are small, usually irregular in outline, never exactly linear, nor do they become markedly orbicular. The margin is irregular in outline, and frequently stellate; sometimes there is also a tendency to become linear, usually associated with radiating projections. The hypothecium is usually more or less dark colored, likewise the epithecium and the upper ends of the somewhat granular simple paraphyses; the epithecium rarely becomes reddish brown.

The spores are characteristic. They are oblong, either colored or colorless, quite constantly four-celled, the ends rounded and one of them narrowed, so that the general outline of the spore resembles that of the sole of a shoe.

The *Arthonias* are southern in their range, though less so than *Graphis*; they occur mostly upon trees, less commonly upon decaying wood.

PLATE 31.

ARTHONIA RADIATA Ach.

1. Natural size.
2. Portion magnified.
3. *Arthonia punctiformis* (nat. size) upon bark of tree; a, apothecia.
4. Section of apothecium.
5. Section of thallus.
6. Paraphyses and spore-sac.
7. Spores.
8. Algae.

6. MYCOPORUM Nyl. Lich. Scand. 291. 1861.

This lowly organized group of lichens is evidently related to the Graphidaceae, though authors do not agree on this point. The only typical representative occurring in the territory is *M. pycnocarpum*, upon the examination of which the following generic description is based.

The thallus is quite rudimentary and although beginning its development below the substratum soon extends over its surface, forming a very deficient crustaceous layer. The algae are quite numer-

ous and are probably *Cystococcus humicola*, although that is not definitely determined, as they also show a close resemblance to *Pleurococcus vulgaris*.

The structure of the apothecia, indicates a near relationship to the Graphidaceae. They are small, irregular in outline, though never distinctly linear; as in the other groups they begin their development below the surface of the substratum which they break through very early, but never project much above it. The hypothecium and epithecium are black; the shape of the paraphyses is very difficult to determine; they seem to form an anastomosing network of slender granular hyphae.

The spores are large, usually colorless or brownish, multilocular and constricted at the middle.

The few representatives of this genus, seem to be southern in their range, occurring upon trees.

PLATE 32.

MYCOPORUM PYCNOCARPUM Nyl.

1. Natural size.
2. Magnified portion.
3 and 4. Section of apothecium and thallus.
5. Paraphyses and spore-sac.
6. Spores.
7. Algae.

7. ARTHOTHELIUM Mass. Mem. Lich. 54. 1853.

In the general structure of the thallus this genus shows a close relationship with those *Arthonias* bearing *Chroolepus umbrina*; in fact many authors combine *Arthothelium* with *Arthonia*, and the general description of the thallus of *Arthonia* applies to it as well.

The apothecia are comparatively large, stellate in outline, agreeing in development and general structure with those of the preceding groups. The epithecium is dark; the entire thecium (exclusive of spore-sacs) and hypothecium is of a dirty brown color, or it may be colorless. The paraphyses are much branched or nearly simple, though their structure is difficult to make out, because of their granular and gelatinous nature. The spore-sacs are large, colorless and somewhat gelatinous at the upper end.

The spores are large, colorless, multilocular and very distinct in outline; there are eight in each spore-sac, which is not usual in genera with such large spores.

This group, of which there are only a few representatives, is somewhat southern in range. The species occur upon trees, most frequently upon the hickories.

PLATE 33.

ARTHOTHELIUM SPECTABILE (Fw.) Stein.

1. Natural size.
2. Portion magnified.
3. Section of apothecium.
4. Section of thallus.
   a, epiphloeodal portion; b, c, d, hypophloeodal portion.
5. Paraphysis and spore-sac.
6. Spores.

Family 5. PHYSCIACEAE.

This family again forms a well-determined and natural group. Its representatives are at once recognized by the spore-characters. The spores are two-celled, the two terminal or nearly terminal plasmic masses are united by a plasmic thread, which character does not exist in any other lichen group. In *Rinodina oreina* this plasmic connection is often not noticeable. In fact, it seems to occur so rarely that I was at first inclined to exclude this plant from the genus. The plasmic connection was, however, quite evident in a number of spores; besides, the general characters of the species indicate that it is closely related to *Rinodina*. It may also be mentioned that various authors have placed *R. oreina* in the genus *Dimelaena*, which is supposed to be characterized by "immersed apothecia." A careful comparative study of the representatives of the genus *Rinodina* soon demonstrates that the apothecia are more or less immersed in the thallus in all of its lower species.

Referring to the key (p. 10) it will be seen that this is the first family in which the thalloid exciple becomes apparent; it is unmistakable in *Theloschistes*, *Physcia* and *Pyxine*, but in *Rinodina* and *Placodium* it is sometimes not very apparent, especially in those forms in which the apothecia are mostly immersed. In nearly all cases a close examination with a lens will reveal the thalloid outer covering of the apothecium which usually extends slightly above the margin of the dark disk.

The generic characters are sufficiently marked, so that it will not be necessary to give any lengthy description of the family characters.

The apothecia are disk-like, rarely immersed in the thallus; the disk is usually flattened or concave, sometimes convex, especially in *Placodium*; the apothecia usually vary from small to medium. A yellow color predominates in the thallus and apothecia of the genera *Placodium* and *Theloschistes* due to a deposition of crystals of some lichen acid in and upon the hyphal cell-walls. *Rinodina* is also more or less impregnated with this coloring material.

The algal symbiont is *Cystococcus humicola* Näg. The fungal symbionts are doubtless derived from one, or, at most, a few ancestral forms of the Patellariaceae (plate 5).

Key to the Genera.

Thallus crustaceous, areolate, margin often foliose and lobed.	
Spores brown; thallus not bright yellow.	1. *Rinodina.*
Spores colorless; thallus yellow to orange.	2. *Placodium.*
Thallus foliose, grey, not yellow.	
Hypothecium dark.	3. *Pyxine.*
Hypothecium colorless.	4. *Physcia.*
Thallus foliose to fruticose, yellow.	5. *Theloschistes.*

1. Rinodina Ach.; Gray's Brit. Pl. p. 448. 1821.

This genus doubtless forms the lowest group of the Physciaceae; it is distinguished from *Placodium* by the uniformly dark-colored spores and the absence of any orange coloration in the thallus; the thallus is grey or greenish in most species; in *R. oreina*, however, it is a pale or dirty lemon or sulphur color, and in *R. chrysomelaena* there is a marked yellowish tinge.

The thallus is usually recognized as typically crustaceous. There is, however, a tendency toward the foliose type, especially near the margin, where lobation is sometimes quite distinct (*R. oreina.*) Sometimes there is a warty structure as in *R. chrysomelaena.* Usually the surface is crustaceous and more or less distinctly areolate; it is always closely adnate and attached to the substratum by means of numerous black rhizoids. The black hypothallus of authors is not sufficiently understood; in many cases it seems to be the remnant of some lichen (usually a related species) over which the *Rinodina* has spread. (Syntrophy of Minks. See parasitic lichens.) Different species of the Physciaceae are frequently in close proximity, especially among the *Rinodinas* and *Placodiums;* there seems to be an inherent tendency to form symbiotic associations.

The apothecia are either immersed in the thallus or sessile; the immersed forms can not be said to have thalloid exciples; but the sessile apothecia are enclosed by a layer of the thallus and should therefore be looked upon as having true thalloid exciples. Usually the apothecia are quite small with flattened disks; in the sessile forms the thalloid margin extends somewhat above the dark disk; in the immersed apothecia the outline of the disk is quite irregular, reminding one strongly of some species of *Buellia* (*R. oreina*). The hypothecium is colorless and not cortical in structure; the outer layer of the thalloid exciple is cortical or semicortical, resembling the cortical tissue of *Physcia*. The spores in the majority of species are dark and typically two-celled as explained in the discussion of the family characters. There are, however, exceptions; in *R. oreina* the connecting plasmic bridge is usually wanting; and it is probable that this species should be classed with the *Buellias* or separately as *Dimelaena oreina* as its spore characters, as well as apothecial characters, strongly point to its exclusion from *Rinodina*. It is not probable that *Buellia* is as closely related to *Rinodina* as Reinke and others seem to think; further study will perhaps demonstrate that discoid sessile apothecia with dark two-celled spores (two cells united by a plasmic bridge) will fully characterize *Rinodina* and that the forms with distinctly immersed apothecia and two-celled spore, the cells of which are not united by a plasmic thread, should be excluded. The algae of *R. oreina* are also different from those of the other species which I have examined, being bright green slightly tinged with blue, rather irregular in form, at least more so than in *Cystococcus humicola* proper; they resemble more nearly *Pleurococcus vulgaris*.

The algae in the remaining undoubted representatives of *Rinodina* are *Cystococcus humicola*. They vary in size in the different species, while their general form remains constant. Ectotrophic haustoria are numerous and are closely adherent to the algae; endotrophic haustoria seem to be comparatively rare.

There are also multisporous forms of *Rinodina* (pl. 34, f. 7.), which according to some authors are included in a distinct genus (*Maronea*).

The *Rinodinas* are quite common throughout the territory and occur upon rocks and bark, less commonly upon soil and moss.

PLATE 34.

RINODINA SOPHODES (Ach.) Nyl.

1. Natural size.
2. A small portion magnified.
3. Section of apothecium.
   a, thecium; b and c, the two layers of the hypothecium; d, upper algal layer; e, medullary layer; f, lower algal layer; g, cortical layer.
4. Section of thallus.
5. Paraphyses and spore-sac.
6. Spores.
7. Paraphyses and spore-sac of *R. constans*.
8. Spores of *R. constans*.

2. PLACODIUM Ach. Lich. Suec. 100. 1798.

This genus, which in many of its characters resembles *Rinodina*, is characterized by the orange color of the apothecial disk; this rarely changing from a rusty red to dark (*P. ferrugineum*). The thallus is usually yellow or orange, rarely grey to dark. The spores are colorless, with terminal plasmic masses, otherwise they are characteristic of the family; they are rarely simple.

The thallus varies from almost typically crustaceous (*P. citrinum*) to typically foliose (*P. murorum*); in general, it may be said that it is more highly differentiated than in *Rinodina*; as in *Rinodina* lobation first shows itself near the margin, the inner portion of the thallus becoming areolate; usually both upper and lower cortical layers are present. In *P. elegans* and other species the mutual adaptation of mechanical and physiological functions are beautifully illustrated (see plate 35); the upper cortical layer is not uniformly thick; at certain areas the tissue is very thin, which allows the algae to approach near the upper surface of the thallus for the purpose of assimilation; the thickened areas supply the necessary mechanical support. The rhizoids are more specialized than in *Rinodina*; the hyphal cells are thicker and more rigid.

In the lower representatives of the genus the thallus is closely adherent to the substratum, but in its higher forms, as *P. elegans*, *P. murorum* and a few others, the thallus-lobes are more or less ascending, approaching in this character the higher groups.

The yellow color is due to the deposition of crystals of chryso-

phanic acid upon the hyphal cells, especially in the upper portion of the thallus as well as in the thecium; on account of this bitter acid, various lichens of this family were used as a substitute for quinine; it is present in nearly all lichens in larger or smaller quantities.

The apothecia are of medium size, typically discoid, and sessile upon the upper surface of the thallus; the thalloid exciple is well developed.

The distribution of the *Placodiums* is much as in *Rinodina*. They seem to be somewhat more specially adapted to substrata of rock but also occur upon bark, dead trees, and old boards. Like the *Rinodinas* they seem to be able to resist a high degree of dryness. The species seem to be fairly well defined though they are sometimes confused with those of *Theloschistes*.

PLATE 35.

PLACODIUM ELEGANS (Link) D.C.

1. Portion of thallus natural size.
2. Portion of a thallus-lobe magnified.
3. Section of apothecium.
4. Section of thallus.
5. Different forms of paraphyses, and spore-sac.
6. Spores.

3. PYXINE Fr. Pl. Homon. 267. 1825.

The spore characters undoubtedly indicate that this genus belongs to the Physciaceae. A contrasting and negative character is found in the black hypothecium; this is so marked that there is a strong tendency to exclude the genus from the family. All the structural characters of the thallus, as well as the apothecia and spores, point to a close relationship to the *Rinodinas*. *Pyxine* is evidently also closely related to *Physcia;* and it seems probable that it and *Physcia* represent two different branches which proceeded from the *Rinodinas*. *Placodium* may likewise have been derived from one of the *Rinodinas*.

The thallus of *Pyxine* as represented by the only two species, *P. picta* and *P. sorediata*, is large, consisting of frequently branching lobes. In *P. picta* the lobes are agglutinate and thin, and they lie flat upon the substratum; the upper surface is light grey to greenish; the lower surface is dark or black, especially in *P. picta;* black rhi-

zoids are quite numerous. The apothecial and spore characters are taken from *P. picta*, *P. sorediata* being, to my knowledge, always sterile. They are in most respects similar to those of the higher forms of *Rinodina;* the paraphyses are shorter and the spores are comparatively few in number; the dark hypothecium is semi-cortical in structure; the hyphae everywhere contain large deposits of crystals of lichen-acid. In the thallus of *P. picta* the upper cortical tissue is deficient; the lower is wholly wanting, its place being taken by a network of hyphae with dark-colored cell-walls.

The thallus of *P. sorediata* is more highly developed than that of *P. picta;* it bears numerous soredia upon the upper surface of the thallus, as well as along the margin. Apothecia never occur; propagation in this species being entirely dependent upon the soredia.

P. picta seems to be southern in its range, while *P. sorediata* is more northern; both occur upon bark and rotten logs.

PLATE 36.

PYXINE PICTA (Sw.) Tuck.

1. Portion of thallus, natural size.
2. Section of apothecium.
3. Section of thallus.
4. Paraphyses and spore-sac.
5. Spores.
6. Algae.

4. PHYSCIA Schreb. Gen. 2: 768. 1791.

The thallus of *Physcia* presents all gradations from nearly crustaceous (*P. adglutinata*), through foliose (*P. stellaris* and the majority of species) to fruticose (*P. ciliaris*, *P. leucomela*). The general characters of *P. adglutinata* indicate the close relationship of *Physcia* to *Rinodina*, from which genus it is doubtless phylogenetically derived. In the majority of the representatives of this genus the thallus is typically foliose with the various tissue-layers well differentiated. The cortical tissue, however, differs considerably from that of *Parmelia* and the majority of foliose lichens, consisting of rather short, much interwoven, closely united hyphal branches, and the walls of the hyphal cells are considerably thickened and gelatinized; intercellular spaces are rare and the cell-lumina are much reduced. Rhizoids are numerous and well developed.

The color of the thallus in most species of *Physcia* is grey, tinged with green above, but having a different color beneath, usually lighter, rarely dark to black; much of the dark coloration of the lower surface is due to the black rhizoids. Growth of the thallus is usually radial; sometimes it becomes eccentrically radial, due to local influences. Branching is usually distinctly dichotomous and very frequent; in the forms with a fruticose tendency the lobes become linear, with the margin lined with long simple or branched cilia (*P. ciliaris*, *P. leucomela*). Some of the species are quite constantly sterile, in which cases they usually bear numerous soredia upon the upper surface of the thallus as well as along the margin of its lobes.

As compared with *Parmelia*, the apothecia are of medium size, sessile, typically discoid with a highly developed thalloid exciple; the thalloid margin usually extends above the disk; in some forms the excipular margin becomes crenate or rugose, in others it remains smooth. In the fruticose forms the margin of the thalloid exciple bears thalloid fringes of considerable size. The disk is dark in color; the spores are in most respects similar to those of *Rinodina*; the color and size is, however, more variable. Some species are said to have four-celled to eight-celled spores, but none of them have come to my notice; it is probable that these are not *Physcias*.

In their distribution the *Physcias*, especially the higher forms, have a southern range. They occur most frequently upon tree-trunks, less commonly upon rocks. Like nearly all the Physciaceae, this group is adapted to a comparatively dry substratum, but for their growth they require a moist atmosphere, at least an atmosphere in which the average percentage of moisture is high; this accounts for the large development of the highly hygroscopic tissue in the thallus (the cortical tissue), which readily absorbs the atmospheric moisture and retains it for the use of the plant. The algae (*Cystococcus humicola*) are intimately enclosed by haustorial branches. Endotrophic haustoria seem to be common in some species, especially in younger and more actively growing plants.

Another characteristic of many of the *Physcias* is the presence of numerous spermagonia, which develop upon the younger portion of the thallus, where they appear as minute black dots. I have found it impossible to employ them in the determination of species, but it is, however, noteworthy that they occur more frequently upon some species than upon others.

PLATE 37.

PHYSCIA SPECIOSA Fr.

1. Natural size.
2. Section of apothecium.
   a, thecium; b, c, the two layers of the hypothecium; d, upper algal layer; e, medullary layer; f, lower algal layer; g, cortical layer.
3. Section of thallus.
   a, colored layer; b, cortical layer; c, algal layer; d, medullary layer; e, lower cortical layer.
4. Paraphyses and spore-sac with spores.
5. Spores.
6. Colorless spores of another species.
7. Algae.

5. THELOSCHISTES Norm.; Tuck. Gen. Lich. 18. 1872.

The question whether *Theloschistes* or *Physcia* is the higher seems to me undecided. As previously indicated the fruticose forms represent the climax of structural development; the fruticose tendency is more marked in this genus, for which reason I consider it the higher, but the plausible objection that the development of *Theloschistes* as a whole is lower than *Physcia* can, however, be raised.

The representatives of this genus are recognized by the presence of a yellow or even orange coloration in the thallus and apothecia, and the fruticose tendency of the thallus. *T. parietinus* is, however, distinctly foliose, although the lobes have a tendency to ascend or to turn upward at the margin. The extreme fruticose development is reached in *T. flavicans*, in which species the thallus-branches are very long, linear, somewhat rounded, showing a marked tendency toward a radial structure. In the majority of species the thallus-lobes are distinctly flattened (centric structure) and comparatively short. In some species the thallus is very short, the lobes are flat and sparingly branched toward the top (*T. polycarpus*). The thallus is attached to the substratum by clusters of root-like rhizoids. In the foliose forms the bunches of rhizoids occur toward the middle portion of the thallus; cilia also occur on the margin of the lobes and apothecia.

The yellow color of the thallus is due to a deposit of crystals of chrysophanic acid, as in *Placodium*, which occurs most plentifully on the upper surface of the younger portions, gradually fading into grey or brown with age. The lower surface is usually pale yellow or grey, likewise showing a shading in color similar to the upper. Black coloration is wanting; the rhizoids are usually grey.

The apothecia are of medium size and are quite common on most species, especially so in *T. polycarpus*, but they are rare or wanting in *T. flavicans*. The formation of soredia is less common than in *Physcia*. In the higher fruticose forms the apothecia are usually terminal, a character which also manifests itself in the fruticose *Physcias*. In the lower fruticose forms and the foliose forms the apothecia may be terminal, on the margin or upon the surface. The disk is yellow or orange in color; the margin of the cup is frequently lined with cilia. In other respects the apothecia resemble those of *Physcia* and *Placodium*.

The spores closely resemble those of *Placodium*, which seems to be strong evidence that this group is phylogenetically derived from that genus.

In their distribution the *Theloschistes* are still more southern than the *Physcias*, and they also have a western range. They occur upon the bark and smaller branches of trees, rarely upon decaying wood, old boards, rocks, etc., frequently in association with species of *Physcia*.

PLATE 38.

THELOSCHISTES CHRYSOPHTHALMUS (L.) Norm.

1. Natural size.
2. Terminal portion of thallus magnified.
3. Section of apothecium.
4. Longitudinal section of thallus.
5. Paraphyses and spore-sac with spores.
6. Spores.

Family 6. PARMELIACEAE.

The limitations and position of this family are dependent upon four essential characters. 1. The presence of the thalloid exciple separates it from the Caliciaceae, Cladoniaceae and Lecidiaceae. 2. The non-union of the spore-plasms excludes it from the Physciaceae. 3. The presence of the discoid apothecium separates it from the Verrucariaceae. 4. The absence of cyanophyceous algae separates it from the Collemaceae and Pannariaceae. It has more nearly the general characters of the Lecideaceae than any other family, those of the apothecia being very much alike.

In this group the fruticose thallus reaches its highest develop-

ment (*Usnea*). The radial structure predominates in *Cetraria*, and in the genera above it. The question may therefore arise as to whether the fruticose or the foliose lichen-thallus presents the highest lichen-type. The answer to this question depends upon whether we consider the mechanical or the physiological function as of prime importance. In the study of *Alectoria*, *Bryopogon*, *Usnea*, in fact of all typically fruticose thalli (*Sphaerophorus*, podetia of *Cladonia*) we find that the mechanical adaptation is highly specialized; the physiological adaptations are, however, not correspondingly developed. In living organisms the physiological function takes precedence over the mechanical function, which suggests the reason why the Collemaceae and Pannariaceae are here placed higher than the Parmeliaceae.

Some of the general characters of the family are the following: The apothecia are discoid with thalloid exciple; but in *Urceolaria* and *Pertusaria* they are more or less immersed in the thallus and can therefore not be said to have a true thalloid exciple; the thallus is usually greenish in color, though there are marked exceptions, as in *Alectoria* and *Bryopogon;* and most of the *Evernias* are tinged with yellow; the spores are quite variable as to the number of septa but quite constant as to size and absence of color; they are medium in size but vary greatly in form. *Urceolaria* is the only genus with multilocular dark spores. The evidence of the spore-characters is in favor of the theory that the spores degenerate as the lichen becomes more highly specialized; this is also well illustrated in the genus *Parmelia*. The higher forms are quite constantly sterile or with very few apothecia, while the lower are constantly apothecium-bearing; it is evident in this genus that the occurrence of the soredia increases with the decrease of the apothecia.

The symbiotic algae are typically *Cystococcus humicola* Näg. They seem to reach their maximum size in the fruticose forms as *Evernia*, *Alectoria* and *Bryopogon;* their maximum increase in number is reached in *Parmelia* and other foliose forms and in the centric thallus-lobes of *Cetraria*.

The fungal portion of the Parmeliaceae indicates a polyphyletic derivation from the Patellariaceae; but which groups of the Patellariaceae represent the ancestral forms from which the various lichen genera were derived is not definitely known. The spermagonia are quite numerous in some of the genera, particularly in *Parmelia* and

Cetraria, usually occurring near the margin or younger portion of the thallus; they frequently occur near the base of apothecia, but I have not found such occurrence to be constant. Sometimes the spermagonia are wholly or almost wholly wanting.

KEY TO THE GENERA.

Thallus crustaceous, areolate, to thickly warty, and minutely foliose.
- Spores multilocular, dark. 1. *Urceolaria.*
- Spores 4–6-septate, acicular, colorless. 2. *Haematomma.*
- Spores simple, colorless. 3. *Lecanora.*
- Spores very minute, numerous. 4. *Acarospora.*

Thallus foliose, lobed or branching.
- Spores two-celled, colorless. 5. *Speerschneidera.*
- Spore simple, colorless. 6. *Parmelia.*

Thallus fruticose.
- Lobes of thallus distinctly flattened.
  - Spores simple, colorless.
    - Thallus-lobes much flattened; structure centric. 7. *Cetraria.*
    - Thallus-lobes less flattened; structure radial. 8. *Evernia.*
  - Spores two-celled, colorless. 9. *Ramalina.*
- Lobes of thallus cylindrical, filamentous, radial in structure.
  - Central hyphal bundle wanting.
    - Spore-sacs with 2–4 spores; exosporium thick. 10. *Alectoria.*
    - Spore-sacs with 8 spores; exosporium normal. 11. *Bryopogon.*
  - Central hyphal bundle present. 12. *Usnea.*

1. URCEOLARIA Ach. Lich. Univ. 74. 1810.

There is some hesitation about placing this group with the Parmeliaceae because of the immersed apothecia. At first it may seem that the prevailing characters point toward the Verrucariaceae, but on closer examination it is, however, found that the apothecia are not globose and that the paraphyses are not gelatinous.

The thallus is crustaceous, usually quite thick, areolate, the areoles becoming distinctly convex, or warty in some species; there is a semicortical upper layer, followed by the algal layer: the medullary layer is well developed and forms the greater thickness of the thallus: there is no evidence of lower cortical tissue. The rhizoidal hyphae

are numerous and differ little from the medullary hyphae or not at all. The prevailing color of the upper surface is gray, the medullary layer is white, as is also the lower surface. The algae, which are doubtless *Cystococcus humicola*, often occur in clusters of from four to as many as twelve, enclosed by a common membrane, but solitary forms are also common, in which respect they differ from the majority of *Cystococci* occurring in lichens.

The apothecia are quite small and occur immersed in the thallus; there is usually one in each areole; rarely two or three, the disk is markedly concave, the excipular margin never extending above the surface of the thallus; sometimes the excipular margin is constricted, thus forming a more or less complete perithecium, which is dark, and the hypothecium is also more or less dark colored, but never distinctly black. The paraphyses are rather long and slender and somewhat granular. The spore-sacs are cylindrical, with the spores usually in a single row.

The spores remain colorless until they are fully formed; in fact the immature colorless spores are larger that the mature dark colored ones. The cause of this secondary reduction in size is not explained; it may be a degenerative process, since the oldest and darkest spores are more or less structureless.

Most of the representatives of the genus are northern in their distribution. The majority occur upon rocks; a few upon the soil.

PLATE 39.

URCEOLARIA SCRUPOSA (L.) Nyl.

1. Natural size.
2. Apothecium and portion of thallus magnified.
3. Section of apothecium.
4. Section of thallus.
5. Paraphyses and spore-sac.
6. Spores. a, colorless immature spore; b, mature spore.
7. Algæ.

2. HAEMATOMMA Mass. Mem. Lich. 32. 1853.

This group is usually combined with *Lecanora*; but it has, however, strongly marked spore-characters, which have led me to maintain the genus. There is no doubt that it is closely related to *Lecanora*, but it is rather difficult to decide whether it is phylogenetic-

ally higher or lower. The thallus seems to be somewhat more highly developed in *Haematomma*, while the thalloid exciple is considerably higher in its development in *Lecanora*. This, however, only applies to the *Haematommas* and *Lecanoras* of the territory, some of the European *Lecanoras* having well-developed foliose thalli and are, therefore, undoubtedly much above the highest *Haematommas*. The apothecial, as well as the spore characters, point to close relationship with *Lecanora* and *Parmelia*.

The thallus is usually regarded as crustaceous. A more or less well-developed upper cortical layer is present in most species; in the lower forms it is scarcely noticeable, consisting of agglutinate hyphae intermingled with the remnants of dead algae. The algae are quite large, considerably larger than the normal or the majority of other lichen *Cystococci*. Endotrophic haustoria are quite numerous.

The medullary layer is well developed, consisting of much branched hyphae, terminating below in the numerous rhizoidal threads. In *H. ventosa* the thallus is very thick, warty and areolate; in the other species, it is comparatively thin. Soredia are numerous in most species, but they do not occur in clusters, being rather evenly scattered over the entire upper surface of the thallus. The color of the thallus is grey, tinged with green, or sometimes yellowish.

The apothecia are medium to sometimes quite large, sessile, or partially adnate to the upper surface of the thallus; they are usually disk-shaped, sometimes irregular in outline, or several disks agglutinate (*H. ventosa*); the disk may be flattened, somewhat concave or convex; the thalloid exciple rarely extends beyond the disk; the outer layer of the thalloid exciple is semicortical, consisting of short hyphal branches placed vertically to the surface and parallel to each other; this layer is considerably thicker than the upper cortical layer of the thallus, with which it is continuous. The excipular algae are few in number and occur only near the cortical layer. The hypothecium is colorless and not cortical, nor is it possible to distinguish more than one layer. The paraphyses are quite slender, sometimes branching: the epithecium and the upper ends of the paraphyses are usually reddish brown in color. The spores are long, acicular, pointed at one end, indistinctly 4-6-septate, curved, undulate or spiral, colorless; they are so characteristic that it is almost impossible to confound them with any others; they resemble most nearly those of *Bacidia*.

The species occur upon rocks, tree-trunks, earth, logs, etc. As to their distribution they seem to be most common in northern latitudes and in mountainous districts.

PLATE 40.

HAEMATOMMA VENTOSA (L.) Stein.

1. Natural size.
2. Section of apothecium.
3. Section of thallus.
   a, upper cortical layer; b, algal layer; c, medullary layer.
4. Paraphyses and spore-sac.
5. Spores.
6. Algae.

3. LECANORA Ach. Lich. Univ., 344. 1810.

The thallus varies from distinctly crustaceous to markedly foliose; in the majority of species occurring in the territory it is crustaceous, varying from thin, to quite thick and, as in *L. tartarea*, closely resembling the thallus of *Haematomma ventosa*. In the higher crustaceous forms and the foliose forms the upper cortical layer is well developed. In the foliose forms (*L. rubina*) there is also a well developed lower cortical layer; the foliose forms also show a decided fruticose tendency as is seen from the ascending lobes and decidedly centric structure (two algal layers). The medullary layer is well developed in the higher crustaceous and foliose forms. The lower surface of the typically foliose thalli bear few or no rhizoids; they are attached by an umbilicus, as in *Umbilicaria* and *Gyrophora*.

Apothecia are usually quite numerous, medium to large, disk-like, sessile with the thalloid exciple extending somewhat above the disk. The margin of the exciple may be entire or rugose and more or less folded. The thecium varies in color from brown to nearly black. The paraphyses are simple, and rather thick. The hypothecium is colorless.

The spores are simple, colorless, elliptical; their form as well as size is somewhat variable; in one species (*L. Sambuci*) they are numerous, there being 12–32 in each spore-sac.

The algae are in all cases *Cystococcus humicola*. In the older portions of the foliose *Lecanoras* the algae begin to disappear so that none can ever be found near the umbilicus; they seem to become quite large, though not very numerous; there is no explanation

advanced for this increase in size; it is perhaps due to excessive nutrition; otherwise they seem normal.

The majority of the representatives of this genus occur in the temperate and north temperate zones, most frequently upon rocks and trees.

PLATE 41.

LECANORA HAGENI Ach.

1. Natural size.
2. Magnified.
3. Section of apothecium.
4. Section of thallus.
5. Paraphyses and spore-sac.
6. Spores.
7. Algae.

4. ACAROSPORA Mass. Mem. Lich. 27. 1853.

Several authors have combined this genus with *Lecanora*, though no logical reason can be assigned for such a procedure, it having few, if any characters in common with that genus.

The thallus is almost wholly wanting in the lower forms; in the higher forms (*A. chlorophana*) it becomes almost distinctly foliose, and lobed, particularly near the margin. In many respects the thallus, as well as apothecia, resemble those of *Haematomma*. The following are the structural characters of the thallus: In most forms, even the lower, there is a decided tendency toward a cortical structure; there is a well defined upper layer of cortical cells extending vertically, which varies in thickness and also somewhat in structure; in all species the outermost cell-layers of the cortical tissue, above and below, are lined with acid crystals to which the characteristic color of the thallus is due, this color being dark in the lower forms and distinctly yellow in the higher. Upon these color-differences sub-genera might be based, but it is, however, not probable that there are sufficient differences to separate them as genera. The hyphal tissue in the algal layer is also more or less cortical. The algae are *Pleurococcus vulgaris* and tend to arrange themselves in vertical rows parallel to the hyphal cells. In the higher species there is a distinct lower cortical layer which resembles the upper cortical layer, though it is thinner; in the lower forms the semicortical medullary tissue gradually merges into the rigid rhizoidal hyphae.

The apothecia are quite variable in size and form, and in all

species are more or less immersed in the thallus. A distinct thalloid exciple exists only in the higher forms. The disk varies from orbicular to irregularly lobate and somewhat folded or crenate; it is usually flattened, more rarely convex, or its margin slightly raised.

The epithecium and upper ends of the simple paraphyses are of the same color as the thallus, that is either dark or yellow. The spore-sacs are long-cylindrical and contain numerous (several hundred, or more) minute, colorless spores.

The *Acarosporas* are quite generally distributed, the majority perhaps occurring in the temperate zones; they grow mostly upon rocks and sandy soil.

PLATE 42.

ACAROSPORA.

1. Natural size.
2. Single apothecium and fragment of thallus magnified.
3. Section of apothecium.
4. Section of thallus.
5. Paraphyses and spore-sac.
6. Spores.
7. Algae. a, as they occur in the thallus; b, normal forms occurring upon the thallus.

5. SPEERSCHNEIDERA Trev.; Tuck. Gen. Lich. 17. 1872.

This is a somewhat doubtful and little-known genus, so far represented by only one species, *S. euploca*. This lichen has certain characters which indicate that it is closely allied to *Parmelia*, but some authors are inclined to consider it more closely related to *Physcia*. Many of its characters point to such a double relationship, but, owing to the incongruity of the spore characters, it cannot be included in the Physciaceae.

The thallus is foliose, with a slight fruticose tendency. It is uniformly and frequently dichotomously branched; the lobes are narrow, linear and of uniform width throughout. The appearance of the thallus is so characteristic that it cannot readily be mistaken; its color is light grey above and below; the lobes are more or less curved upward, so that they only come in contact with the substratum at certain areas, at which the rhizoids occur.

Upon microscopical examination of the thallus it is found that the upper and lower cortical layers are enormously developed, while the

medullary layer is much reduced. This is no doubt for the purpose of supplying the necessary mechanical support to the slender branches. The algae (*Cystococcus humicola*) are quite numerous and rather small. The air enters the thallus at the sides, where the cortical tissue is very thin and is traversed by breathing canals.

The apothecia are of medium size, sessile upon the upper surface of the thallus near the middle, hence the older portions; the thalloid exciple scarcely reaches above the flattened disk; the epithecium is light brown and the hypothecium colorless, very thick, cortical in structure, and is divided into two layers; in the upper the cells are elongated at right angles to the surface of the disk; in the lower, which is by far the thicker, the cells are elongated vertically to this surface.

The paraphyses are simple and colorless. The spores are rather small, elliptical, colorless and distinctly two-celled; the two cells are not, however, united by a plasmic thread, which excludes the genus from the Physciaceae.

S. euploca seems to be southern and western in its distribution, and is certainly very rare in the eastern United States. It occurs upon rocks. The specimens which came to my notice were associated with a species of *Collema*.

PLATE 43.

SPEERSCHNEIDERA EUPLOCA (Tuck.) Trev.

1. Thallus natural size. a, apothecia.
2. Portion of thallus magnified.
3. Section of apothecium.
4. Section of thallus.
5. Paraphysis and spore-sac.
6. Spores.
7. Algae.

6. PARMELIA Ach. Lich. Univ. 89. 1810.

It is highly probable that this group is phylogenetically derived from *Lecanora*, as there is certainly a close similarity between the higher *Lecanoras* and lower *Parmelias*.

The thallus in this genus is foliose and shows a distinct dorsiventral structure. There is no indication of any fruticose tendency. In the majority of representatives dichotomous branching of the

thallus is very marked (ex. *P. centrifuga*), in others (*P. perlata*, *P. rudecta*, *P. latissima*) the lobes are very large and the dichotomous branching is not distinct, even approaching the entire form. Branching of the thallus is, however, characteristic of the genus, in this respect approaching the characters of the thallus in *Physcia*, but in general it is larger and shows higher specializations. The prevailing colors of the upper surface are greenish grey and greenish brown; the lower surface is brown to black, usually bearing black rhizoids; cilia sometimes occur along the margin. Soredia are also numerous on the upper surface of the thallus as well as along the margin. Sometimes numerous isidioid branches form nearest the middle of old thalli (especially in *P. Borreri*), finally nothing remaining but a broken-down thallus bearing them in large numbers; there is no doubt that these outgrowths serve as vegetative propagative organs, similar to the soredia.

Both upper and lower cortical layers are present and are far more characteristically cortical than in any of the genera heretofore described. The cells are considerably shortened, with firm walls and rather large lumina. The algal layer is clearly defined. The medullary layer consists of a loose network of hyphae especially adapted to act as an aërating tissue. In some species (*P. physodes*) there is a highly specialized aërating tissue, consisting of an air-space just above the lower cortical layer.

The apothecia vary from medium to very large; they are sessile upon the upper surface of the thallus; in general it may be stated that they are comparatively rare, especially in those forms with numerous soredia. The enormous development of the thalloid exciple would make it seem probable that the prime significance of this structure is to aid in assimilation rather than in reproduction by spore formation; each apothecium is in reality a secondary thallus having a combined radial and centric structure; the epithecium is usually brown in color; the paraphyses are simple, very rarely branching, rather rigid with slight coloration at the upper ends; the hypothecium is colorless and consists of two, usually more or less distinct layers, much as in *Speerschneidera*.

The spores are simple, colorless, elliptical and quite constant in size and form; they very frequently contain two oil-globules which to casual observance presents the appearance of a two-celled spore; the spore-wall is perfectly colorless, quite thin and somewhat gelatinous.

Most of the representatives of this genus are fairly well characterized; some critical study is, however, necessary to settle disputes in regard to many of the supposed "varieties" and "forms."

They are almost cosmopolitan in their distribution. The majority of species perhaps occur in the north temperate zone and live upon rocks and trees; some species show a preference for the rougher barks, while others seem to have no choice.

PLATE 44.

PARMELIA PERLATA (L.) Ach.

1. Plant natural size.
   a, apothecia; b, lobe of thallus; c, soredial patches.
2. Section of apothecium.
   a, thecium; b and c, the two layers of the hypothecium; d, upper algal layer; e, colonies of algae scattered through the medullary layer; f, lower algal layer; g, lower cortical layer.
3. Section of thallus.
4. Paraphyses and spore-sac.
5. Spores.
6. Algae and haustoria.

7. CETRARIA Ach. Meth. Lich., 35. 1803.

It is highly probable that this genus is phylogenetically derived from *Parmelia*, or it may bear the same relation to *Lecanora* that *Theloschistes* does to *Placodium*; that is, it may be looked upon as a fruticose branch derived from *Lecanora* or from *Parmelia*.

The thallus-lobes are in all cases distinctly flattened. In the majority of species a centric structure is evident. In some cases the thallus lies quite flat and has a dorsiventral (bifacial) structure (*C. juniperina*). The upper and lower cortical tissues are well developed in both the centric and dorsiventral thalli; in the former there are, however, two algal layers, while in the latter there is only one. Rhizoids are few or wanting, even in the horizontal thalli; cilia are, however, frequently present (*C. Islandica*). Many of the *Cetrarias* also contain a high per cent. of acid crystals (cetraric acid) deposited in and upon the hyphal cell-walls. The color of the thallus is quite variable; it may be brown (*C. Islandica*), yellow or yellowish (*C. juniperina*), or almost coal-black (*C. Fahlunensis*).

The apothecia are medium to large, sessile upon the upper sur-

face of the thallus, but in the majority of species are few or wanting. The disk is quite thin, margin somewhat torn or crenate, with a brown shining epithecium. The colorless hypothecium is divided into two well-marked more or less cortical layers. The paraphyses and spore-sacs are very short; the spores small, otherwise as in *Parmelia*; the thecium of *Cetraria* resembles in all respects a reduced thecium of *Parmelia*.

Soredia are not of such frequent and plentiful occurrence as in the preceding genus, which gives the thallus a somewhat smoother aspect. The thallus is also more brittle than in *Parmelia*, due to the greater development of the cortical layers, with a corresponding reduction of the medullary tissue.

Most of the *Cetrarias* are northern; they occur upon trees, soil and rocks of the higher altitudes and latitudes; their distribution east and west seems to be about uniform. Most of the European forms occur in North America, but a few American species do not occur in Europe.

PLATE 45.

CETRARIA JUNIPERINA (L.) Ach.

1. Portion of the thallus natural size.
2. Section of apothecium.
3. Section of thallus.
4. Paraphyses and spore-sac.
5. Spores.
6. Algae.

8. EVERNIA Ach. Lich. Univ. 84. 1810.

This genus has very likely been derived from *Cetraria*. We have here a markedly higher differentiation of the fruticose type; the lobes have become much narrowed and in the majority of species are somewhat cylindrical and as a natural consequence show a radial arrangement of the tissue-elements.

Branching of the thallus is often dichotomous with an acropetal decrease in the size of the lobes (*E. vulpina* and others). In the forms with a foliose tendency the lobes are more uniform in size (*E. furfuracea*). The thallus never has that smooth shining appearance so common in *Cetraria*; the outer surface appears as though covered with a very fine powder, due to the presence of a considerable de-

posit of acid crystals (vulpinic acid) in and upon the cells of the outer semicortical layer. Soredia and isidioid branches are also frequently present, particularly in *E. vulpina* and *E. furfuracea*.

The general structure of the thallus is as follows: The outermost protective covering consists of an irregular network of hyphal cells which usually extend in a direction vertical to the outer surface; the cell-walls are much gelatinized and lined with the above mentioned deposit of acid crystals; next follows the algal layer, which consists of *Cystococcus humicola* surrounded by the haustorial branches; the algae, while few in number, are comparatively large, no doubt due to hypernutrition; still more internally is found the medullary layer, usually associated with the special mechanical tissue; the central area is either hollow, or filled with a loose hyphal tissue, the cells of which are more or less interwoven; the mechanical tissue consists of hyphal bundles, the cells of which extend parallel with the longitudinal axis of the thallus; these bundles occur at regular intervals, forming a broken ring as seen in cross section; sometimes this ring becomes more or less continuous, approaching in structure the hollow cylinder; the mechanical tissue is especially adapted to resist both longitudinal (pulling) and lateral tensions. In some species this special mechanical tissue is wanting, the necessary mechanical tissue being supplied by the external cortical layer, while the entire interior is filled by the loose medullary tissue.

The color of the thallus varies from greenish grey (*E. furfuracea*) to brilliant yellow (*E. vulpina*). Various fungal parasites are not uncommon upon the thallus of *E. vulpina* and other species besides the spermagonia.

The apothecia are usually terminal, or nearly so, large, the disk flattened with a more or less irregular outline; the margin (excipular) often bears small thalloid branches; the thecium is brown to dark brown. The paraphyses and spore-sacs are much as in *Cetraria*, likewise the spores. The hypothecium is colorless and usually consists of two distinct layers.

The *Evernias* are typically western, most of them being limited to the Rocky mountains and Pacific coast region, where they occur upon trees and rocks. Only the sterile form of *E. vulpina* occurs in our territory.

PLATE 46.

EVERNIA VULPINA (L.) Ach.

1. Portion of thallus natural size.
2. Section of apothecium.
   a, thecium; b and c, layers of the hypothecium; d, algal layer; e, medullary tissue; é, mechanical tissue (hyphae); f, algal layer; g, protecting and mechanical tissue.
3. Radial transverse segment of thallus.
   a, outer covering corresponding to 2 g; b, algal layer; c, medullary tissue; d, mechanical bundle cut transversely.
4. Paraphyses and spore-sac.
5. Spores.

9. RAMALINA Ach. Lich. Univ., 122. 1810.

The phyletic relationship of this group is as yet undetermined. According to the spore-characters it is not derived from the *Lecanoras* or *Parmelias;* some authors regard it as closely related to *Rocella* but it is morphologically quite different.

The position of the genus is also somewhat uncertain. Microscopically considered, some of the forms (*R. linearis*) are closely related to *Usnea*, and hence higher in position than *Evernia*. Its mechanical adaptations seem to indicate a lower position.

The thallus, although fruticose in all the species, always remains flattened. In this genus we have the centric structure well characterized, with a radial tendency in some of the forms. The tissue-layers are quite constant throughout the genus and are essentially as follows: An outer layer, quite well developed, consisting of closely agglutinate hyphae extending parallel to the long axis of the thallus; sometimes this tissue is interwoven with hyphae which extend for the most part radially horizontal; this layer constitutes the protective and mechanical tissue, differing quite materially from the outer layer in *Evernia*, not only structurally, but also in the absence of the numerous acid crystals, which accounts for the comparative smoothness of the outer surface of the *Ramalina* thallus; next follows the algal layer, in which the algae (*Cystococcus*) occur in colonies, considerably larger than in *Evernia*, otherwise much the same. The entire interior is occupied by a medullary tissue, consisting of loosely interwoven hyphae. It should, however, be remarked that occasionally there are a few scattered mechanical hyphae nearer the algal

layer, which always extend in a longitudinal direction and which perhaps indicate the beginnings of mechanical bundles, similar to those in *Evernia*.

The apothecia are small to medium and occur upon the upper surface of the thallus, along the margin or sometimes terminal; the disk is flattened, convex or concave; the excipular margin is entire, without cilia or thalloid fringes; the hypothecium is colorless, consisting of much interwoven hyphae; the two layers are rather indistinct. The paraphyses and spore-sacs are somewhat longer than in *Evernia* and *Cetraria*. The thecium is usually light-brown or almost of the same color with the thallus.

The spores are quite small, colorless, two-celled, elliptical, sometimes somewhat curved.

The representatives of this genus are southern and western in their distribution, occurring upon trees, rocks and sandy soil. Some of the tree forms attain an enormous size (*R. reticulata*, *R. linearis*). Only comparatively few of the species occur in the territory, and of these *R. calicaris* is most frequent.

PLATE 47.

RAMALINA CALICARIS (L.) Fr.

1. Natural size.
2. Portion of thallus with apothecia.
3. Section of apothecium.
4. Longitudinal section of thallus.
5. Paraphyses and spore-sac.
6. Spores.
7. Algae.

10. ALECTORIA Ach. Lich. Univ. 120. 1810.

This genus differs from the foregoing in its cylindrical radially built thallus, and its large spores with thick walls.

The thallus is in all cases typically fruticose, never showing any foliose tendency. Branching is frequent and more or less distinctly dichotomous, with a gradual decrease in the size of the branches in an acropetal direction. At the points of branching the thallus is somewhat flattened for the purpose of supplying mechanical support.

In this group the mechanical (and protective) tissue is highly developed and specially adapted to resist lateral tensions, that is

the mechanical tissue is arranged on the plan of a hollow cylinder, with a secondary adaptation to resist longitudinal tensions. The structure is comparatively simple and is essentially as follows: The outer mechanical tissue consists of a continuous layer of closely agglutinate hyphae extending in a longitudinal direction; occasional branches are irregularly interwoven between these; the cells of the hyphae situated toward the outer surface tend to become cortical in structure, and are often more or less colored, even becoming entirely black; deposits of acid crystals are very plentiful throughout the entire hyphal structure; this mechanical layer is quite thick, forming by far the greatest bulk of the substance; the hyphal walls are very thick, gelatinous and become brittle when dry; the algal layer which follows next is very deficient, consisting of rather minute, sparingly scattered clusters of algae suspended in a very loose and deficient medullary tissue. The interior is not hollow, though the hyphal tissue is sparingly developed.

In *A. sarmentosa* the entire thallus bears oval soredial patches which apparantly serve a two-fold purpose, that of supplying a means of vegetative propagation and of admitting air into the interior.

The color of the thallus varies from light to black. This variation may be observed in the same plant at different periods of its development (*A. sarmentosa*).

The apothecia are few, of medium size, sessile upon the sides of the thallus. The hypothecium is colorless and consists of two distinct layers of semicortical tissue; sometimes a third intermediary layer is noticeable, forming a sort of transition layer between the upper and lower layers. The spore-sacs and simple paraphyses are of medium size and length.

The spores are simple, rather large, usually two in each spore-sac. The spore-wall is divided into two distinct layers (exosporium and endosporium) which are of considerable thickness. The size and thickness of the wall at once distinguish these spores from those of related groups. They are usually described as colorless, but they become distinctly brown (smoky-brown) with age; they do, however, remain colorless for a considerable time.

The *Alectorias* are confined to the arctic and subarctic zones, and to mountainous districts. Only a few species have so far been reported from our territory. They occur upon trees and rocks.

PLATE 48.

ALECTORIA SARMENTOSA Ach.

1. Portion of thallus natural size.
2. Section of apothecium.
   a, thecium; b, c, d, three layers of the hypothecium; d, algal and medullary layer; f, protective layer.
3. Transverse radial section of thallus.
   a, outer layer of longitudinal hyphæ; b, algal layer; c, medullary tissue.
4. Paraphysis and spore-sac.
5. Spores.

11. BRYOPOGON Link. Handb. 3: 164. 1833.

This group is very closely related to *Alectoria* in the structural arrangements of the thallus. The essential differences are found in the spore-characters.

The thallus is in all cases typically fruticose and radial in structure; the outer mechanical and protective layer resembles that of *Alectoria* in structure, but differs in being considerably thinner and in the meagre deposit of acid crystals. The cell-walls of the outermost hyphae become dark to black in color; the algae are distributed as in *Alectoria*. The central medullary tissue of loosely interwoven hyphae is traversed by a few mechanical bundles consisting of several agglutinate hyphae extending longitudinally; these give additional support to resist longitudinal (pulling) tensions, which is highly essential, since the thalli in most species are very long and slender.

The thalli are also somewhat flattened at the points of branching; soredia are common in some species; the prevailing color of the thallus is black, the long slender forms closely resembling coarse black hair; branching is dichotomous and usually less frequent than in *Alectoria*.

The apothecia are very few and sessile upon the sides of the thallus. The spore-sacs and paraphyses are quite short, the hypothecium colorless and separable into two layers; the disk is entire, somewhat irregular in outline; the epithecium is of a lighter color than the thallus; the spores are very small, colorless, simple, eight in each spore-sac. Owing to the fact that forms of *Alectoria* and *Bryopogon* are very frequently sterile, one is apt to confuse the genera;

the structural differences of the thallus may therefore be of significance in separating them.

The representatives of this genus are also mostly northern, occurring upon trees, rocks and fences. Most of the American species occur north and west of our territory.

PLATE 49.

BRYOPOGON FREMONTII (Tuck.)

1. Portion of thallus natural size.
2. Portion of branch with apothecium magnified.
3. Section of apthecium.
4. Radial transverse section of thallus.
   a, outer protective and mechanical tissue of longitudinal hyphae; b, medullary tissue; c, mechanical bundles of longitudinal hyphae.
5. Paraphysis and spore-sac.
6. Spores.

12. USNEA Adans. Fam. Pl. 2: 7. 1763.

The *Usneas* are at once recognized by the well developed central mechanical bundle of hyphae; they represent the acme of development in the fruticose thalli, both as to size and functional as well as morphological specialization.

The fruticose thallus is frequently branched, cylindrical, without being flattened at the points of branching. The branches usually form an angle approaching 90°. A section reveals the following structures which are quite constant in all the representatives of the genus. An outer semicortical tissue, whose exact structure is rather difficult to make out, owing to the fact that cell-walls are quite indistinct; it consists of agglutinate, somewhat cortical hyphal cells, which for the most part extend vertical to the surface; it is practically impossible to determine the exact outline of the individual cells, and the difficulty is increased by the presence of acid crystals deposited upon the cell-walls, particularly toward the outer surface. This layer is followed by the algal layer, which consists of groups of algae, held together by the haustorial branches; as in *Alectoria* and *Bryopogon* the algae are comparatively few in number. The third layer constitutes the medullary tissue which consists of a loose network of hyphae. In the middle occurs the mechanical bundle of elongated hyphae, which is sometimes separated from the medullary layer by

a thin covering of much-branched rather small-celled hyphae, a tissue comparable to the endoderm or root-sheath of higher plants.

The prevailing color of the thallus is light green to grayish green, sometimes changing to a reddish brown. In a few species, especially *U. barbata*, the main branches are covered by minute secondary thalli which never bear apothecia; these are for the purpose of increasing the assimilating surface and are functionally comparable to the leaves of higher plants. Soredia sometimes occur.

As a rule the apothecia are few; sometimes, however, individuals occur on which they are numerous (*U. barbata*); they are large and usually terminal. The disk is much flattened and thin, the margin bearing numerous small thalloid branches and sometimes somewhat torn; the epithecium is of about the same color as the thallus; thecium and hypothecium are colorless. The spores are simple, colorless, without any special characters.

The *Usneas* are somewhat northern in their distribution; *U. barbata* seems to be quite cosmopolitan; they occur most frequently upon trees.

PLATE 50.

USNEA BARBATA (L.) Fr.

1. Small portion of thallus natural size.
2. Section of apothecium.
3. Radial longitudinal section of thallus.
4. Paraphyses and spore-sac.
5. Spores.

Family 7. VERRUCARIACEAE.

This family is quite definitely limited by its apothecial characters. The apothecium is more or less spherical and disk closed. In the lower forms (*Trypethelium*, *Pyrenula*) the apothecia are partly or almost entirely hypophloeodal. In the higher forms (*Dermatocarpon*, *Endocarpon*) the apothecia are immersed in the thallus. In the intermediate forms (*Conotrema*, *Thelotrema*, *Verrucaria*) they are sessile upon the substratum and partially enclosed by the rudimentary thallus. In the non-foliose forms the thallus is mostly hypophloeodal. The paraphyses have a tendency to become gelatinized, especially in the higher forms (*Verrucaria*, *Dermatocarpon*, *Endocarpon*). In the lower forms the paraphyses are long, slender and very soft or partially gelatinized. Older lichenologists have

even stated that some of the groups are devoid of paraphyses, which is, however, not the case, as closer examination will clearly show. Frequently the cell-walls of the paraphyses are so much gelatinized that their outline is not distinguishable; in such cases it is usually possible to trace the direction of the cells by the granular plasmic contents.

The great differences in the spore characters indicate a polyphyletic origin. The fungal ancestors are doubtless to be found in the Pyrenomycetous groups Sphaeriaceae and Massariaceae.

Two forms of algae predominate in this family. *Chroolepus umbrina* occurs in the genera from *Trypethelium* to *Verrucaria*. Exceptionally *Cystococcus humicola* occurs in certain species, whether constantly or not I am at present unable to state. *Pleurococcus vulgaris* Menegh. occurs in *Verrucaria*, *Dermatocarpon* and *Endocarpon*, where it seems to have become greatly modified in size and form (see Thecial Algae); it may, however, be possible that the alga is not *Pleurococcus vulgaris*, though the culture experiments of Stahl and others seem to prove that such is the case.

It is also evident that many intermediate forms of this family are wanting, as, for instance, the connecting links between *Verrucaria* and *Dermatocarpon* and between *Dermatocarpon* and *Endocarpon*. In the former the intermediate forms between rudimentary crustaceous thallus and typical foliose thallus are wanting; the difference between the thallus of *Dermatocarpon* and that of *Endocarpon* is principally that of size; yet it seems evident that there must have been intermediate forms.

Key to the Genera.

Thallus crustaceous, often hypophloeodal.
- Spores 6–8 celled, colorless. — 1. *Trypethelium.*
- Spores 4-celled, brown. — 2. *Pyrenula.*
- Spores many-celled. — 3. *Conotrema.*
- Spores multilocular, colorless.
  - Exosporium normal. — 4. *Thelotrema.*
  - Exosporium thick, gelatinous. — 5. *Gyrostomum.*
- Spores simple, colorless.
  - Spores medium size. — 6. *Verrucaria.*
  - Spores very large. — 7. *Pertusaria.*

Thallus foliose.
- Spores multilocular, colorless. — 8. *Dermatocarpon.*
- Spores simple, colorless. — 9. *Endocarpon.*

1. Trypethelium Spreng. Kennt. d. Gewächse, 3: 350. 1804.

This group takes the same position in the family that *Mycocalicium* does in the Caliciaceae. Some of the representatives are very doubtful lichens. In all of the species occurring in the territory the thallus is very rudimentary and entirely hypophloeodal. Careful sectioning and searching is necessary to detect any algae (*Chroolepus umbrina*), which occur in small clusters distributed about the base of the apothecia. The thallus can not be said to have any structure. There is simply a meagre hyphal network, continuous with the hyphae of the apothecium, which encloses the algae; the filaments are slender, much branched and much contorted. Tuckerman and others describe the structure and macroscopic appearance of the thallus, which plainly shows that these authors had in mind the secondary color-changes in the substratum (bark), and not the thallus. The network of hyphae holding the algae occurs in the intercellular spaces of the bark. Neither of the symbionts ever penetrate the intact cork cells. The chemical changes causing the modifications in color of the bark have not been satisfactorily explained, but they are doubtless due to acids secreted by the lichen.

The apothecia are likewise entirely hypophloeodal. They occur in clusters of five to forty or even more. Each apothecium is, however, entirely free from the neighboring ones and may be considered as an individual belonging to the colony; the outlines of these colonies are very irregular. The apothecium is globular in form and simple in structure. The dark to black hypothecium and proper exciple (perithecium) at first entirely enclose the thecium consisting of long, simple, slender, soft, more or less gelatinous paraphyses and the spore-sacs. As the apothecia grow they push up the superimposed layer of bark, producing a warty appearance of the surface. At maturity the excipular opening (ostiole) widens more and more; finally a small pore-like opening is also formed in the layer of cork which allows the spores to escape. The paraphyses are highly hygroscopic and there is little doubt that they play an important part in forcing up the layer of bark as well as in ejecting the spores. The covering of bark performs the function of the cortical layers in the higher lichens, that is, it forms a mechanical protection for the rudimentary thallus and the young growing apothecia. The corky covering immediately above the apothecia is of a dark rusty color, which gradually fades into the brownish or greenish color of the area over the thallus.

The spores are normally colorless and eight-celled; in form they are spindle-shaped; the plasmic portions are somewhat diamond-shaped, two obtuse angles closely approaching each other near a transverse septum.

Much confusion exists in the limitation of this genus, some authors uniting *Trypethelium* and *Pyrenula* in one, but it seems more consistent to keep them separate, since the spore-characters are very marked in both genera; only a very few species occur in the territory; many of the forms described as *Trypethelium* belong to *Pyrenula*.

This genus is essentially southern; the species occur upon trees, forming patches of considerable extent; they are evidently closely related to some of the Sphaeriaceae; the immediate fungal ancestors require further study.

PLATE 51.

TRYPETHELIUM VIRENS Tuck.

1. Plants natural size. a, apothecial colony.
2. Semidiagramatic section through apothecia and substratum (magnified) a, apothecium developing below the substratum; b, mature apothecium.
3. Section of apothecium.
4. Algae and hyphae of the very rudimentary thallus.
5. Paraphyses and spore-sac.
6. Spores.

2. PYRENULA Ach. Lich. Univ. 64. 1810.

This genus closely resembles *Trypethelium*. The thallus and apothecia are hypophloeodal, the latter opening by a pore at maturity. In by far the greater number of species the thallus is quite as rudimentary as in the preceding genus, but in the higher forms the algal colonies (*Chroolepus*) are quite apparent. The fungal ancestors are evidently derived from the Sphaeriaceae. In fact, there is little doubt that many herbarium specimens catalogued as species of *Pyrenula* are really fungi; careful study of the specimen is necessary to demonstrate the absence or presence of a thallus.

In the majority of the representatives of the genus the apothecia are quite uniformly scattered; in some they form colonies, as in *Trypethelium*. The superimposed corky layers of the substratum un-

dergo a change in color, usually becoming grey, brown or dark brown, especially over the apothecia; as in *Trypethelium*, the thallus never becomes visible to the naked eye. The hypothecium and exciple are quite constantly dark in color, consisting of a network of hyphae with dark cell-walls. The paraphyses are colorless, shorter than in *Trypethelium*, slender, with a decided tendency to become gelatinous or granular. The spore-sacs are quite slender and cylindrical.

The spores are usually more or less colored and constantly four-celled, otherwise resembling those of the preceding genus; some forms seem to have spores devoid of color; it may be, however, that these represent immature conditions. It should also be remarked that the young, undeveloped spores of *Trypethelium* are four to six-celled and also that all the younger spores of *Pyrenula* are colorless.

The representatives of this genus are southern in their distribution, though quite a number occur in our territory; they live upon the smoother barks where they form colonies of considerable size. In their habit they do not seem to differ materially from the closely related fungi (Sphaeriaceae). The symbiotic relationship is as yet in a rudimentary stage; it would be interesting to determine if any of the *Pyrenulas* can develop apothecia without the symbiotic algae.

PLATE 52.

PYRENULA NITIDA Ach.

1. Plants natural size. a, apothecia.
2. Single apothecium enlarged.
3. Section of apothecium.
4. Algae and hypae
5. Paraphyses and spore-sac.
6. Spores.

3. CONOTREMA Tuck. Syn. Lich. 186. 1848.

The present position of the genus is very doubtful; it has no characters which will give it a definite position in any of the nine families. Its apothecial characters place it nearest the Verrucariaceae; the algae are, however, foreign to this family, for instead of *Chroolepus* they are *Cystococcus*. Exceptions of this kind occur elsewhere and therefore need not be considered of special impor-

tance. Some authors consider this group very closely related to *Urceolaria*; the apothecial characters are, however, essentially different.

The thallus is mostly epiphloeodal, particularly the older portion, crustaceous, thin, somewhat areolate; the algae (*Cystococcus humicola*) very rarely occur below the surface of the substratum; the thallus is attached to the substratum by comparatively long sparingly branched hyphae, which are easily torn loose by heavy winds and rains; thus it happens that a considerable portion of the thallus is removed, bringing into greater prominence the more firmly attached globose apothecia.

The apothecia are comparatively large, with a dark perithecium (hypothecium and proper exciple). The pore is quite large and begins to form early in the development of the apothecium. The apothecium is partly hypophloeodal; very early in its development it breaks through the thin layer of superimposed cork-tissue.

The paraphyses are comparatively long, slender, and sparingly branched near the apex; they also show a decided tendency to become granular. The spore-sacs are quite large, cylindrical, each containing eight long colorless spores. It is impossible to confuse these spores with any others; their extreme length, cylindrical form and numerous transverse septa are striking.

Only one species has so far been reported, which seems to occur throughout the territory upon trees with comparatively smooth bark, such as *Betula* and *Acer*.

PLATE 53.

CONOTREMA URCEOLATUM Tuck.

1. Natural size. a, apothecia.
2. Apothecium and fragment of thallus magnified.
3. Section of apothecium.
4. Section of thallus.
5. Paraphyses and spore-sac.
6. Spores. a, exosporium; b, cell-lumina.

4. THELOTREMA Ach. Lich. Univ. 62. 1810.

This is another group whose position in the system is not definitely determined. Many of the characters met with in *Conotrema* also present themselves here.

As in the former genus the thallus is quite rudimentary and partly

hypophloeodal; the algae, which are *Chroolepus umbrina*, are rather sparingly scattered about the apothecium and still less sparingly over the substratum or just beneath its surface. The hyphae are slender and much branched with very indistinct septa, penetrating deeply into the substratum. A hyphal branch enters into the interior of a cork cell through the small pores and destroys parts of the cell-wall. The necessary mechanical protection to the thallus is supplied by the superficial cork layers of the substratum which are, however, broken here and there, thus allowing the thallus to spread over the surface. The hyphae are intimately united with the algae, but I have not been able to find any evidence that they penetrate the algal cell-wall.

The apothecia are very striking in appearance. They resemble in all respects a miniature volcanic crater (*T. lepadinum*); this character alone will enable one to recognize the genus; they are usually very numerous, quite uniformly scattered over the thallus, and begin their development below the surface of the substratum, somewhat more superficially than in *Pyrenula* and *Trypethelium*. The superimposed corky tissue is forced upward by the hygroscopic paraphyses. At an early period the spores begin to form, and at maturity are of considerable size. The exciple early in the history of the apothecial development separates from the rigid cone formed by the corky cells and the hyphae, and at maturity the hypothecial disk alone remains attached to the substratum; the inflexibility of the cone and the alternate loss and gain of water of the thecium causes the separation of the greater portion of the perithecium. In the dry state the excipular fringe is plainly visible within the hollow of the cone; on the absorption of moisture the excipular margin is forced against the sides of the cone, which projects above the disk and the excipular margin. The paraphyses are long, simple, slender and highly hygroscopic. The absence of color throughout the entire plant is noteworthy.

The spores are large, multilocular, colorless, long spindle-shaped, with a rather thick gelatinous outer wall, which is more or less rugose, particularly in *T. lepadinum*.

The above generic description is taken from *T. lepadinum*, which is, perhaps, the only species occurring in the territory.

The representatives of this genus have a decidedly southern range and grow upon the bark of various trees.

PLATE 54.

THELOTREMA LEPADINUM Ach.

1. Natural size.
2. Two apothecia and fragment of thallus magnified. a, raised portion of thallus and substratum; b, excipular fringe.
3. Section of apothecium.
4. Section of thallus.
5. Paraphyses and spore-sac.
6. Spores.

5. GYROSTOMUM Fr. Pl. Homon. 268. 1825.

This genus is represented by one species (*G. scyphuliferum*), very simple in its structure, with well-marked and apparently constant characters.

As in the preceding, the thallus and apothecia begin to develop below the surface of the substratum. The thallus, especially the algae, remain almost entirely hypophloeodal; only a few algae (*Chroolepus umbrina*) exist, about which the slender hyphae form a close network; there is no distinction into layers. The alga-bearing hyphal network extends between the separated cell-layers of the superficial cork, never penetrating the intact cells of the substratum.

The apothecia are quite small and semi-globose; they begin their development below the surface of the substratum but soon break through, and about this time the apical pore begins to form; it increases considerably in size, so that at maturity the apothecia are more or less urn-shaped. The hypothecium (perithecium) is black, likewise the epithecium. The paraphyses are simple and considerably gelatinized.

The spores are multilocular, colorless, with a thick gelatinous exosporium.

This lichen is of southern range, occurring upon various trees.

PLATE 55.

GYROSTOMUM SCYPHULIFERUM (Ach.) Fr.

1. Natural size.
2. Portion magnified.
3. Section of apothecium.
4. Section of thallus.
5. Paraphyses and spore-sac.
6. Spores. a, young spores; b, later stage; c, mature spores.
7. Algae.

6. Verrucaria Wig. Prim. Fl. Hol. 85. 1780.

The representatives of this genus are unquestionably lichens; the thallus, though crustaceous, is usually well developed; there is, however, great confusion among authors as to the limitations of the genus; some include species with simple, two-celled, and many-celled to multilocular spores, both colorless and colored; such variability in spore-characters associated with imperfect descriptions of the thallus (algae in particular) has caused a great difficulty in attempting to determine supposed species of *Verrucaria*. In order to avoid this I have included under *Verrucaria* all lichens having the following characteristics.

The thallus is crustaceous but shows a high degree of differentiation, as is indicated by the hyphal structure and its relation to the algae; the hyphal tissue is semicortical in structure, consisting of closely united short cells, much like those of *Acarospora*; the algae are *Pleurococcus vulgaris* and have much the position and general arrangement in the thallus that they do in *Endocarpon*, to which genus *Verrucaria* is phylogenetically related. All the species examined contained *Pleurococcus*, though according to some authors *Chroolepus umbrina* is supposed to be typical of the genus.

The apothecia are very small, almost entirely immersed in the thallus and substratum; the perithecium (hypothecium and excipular margin) is quite dark in color due to a deposition of lichenic acid within and upon the hyphal cell-walls; the paraphyses are comparatively short and almost entirely gelatinized, so much so that some authors have cited the absence of paraphyses as a generic character; close examination will demonstrate that this is not the case; the spore-sacs are also much gelatinized and contain eight colorless simple spores; the spore-wall is thin; the plasmic contents are granular and mixed with oil globules; the whole presents the appearance of degenerative products. It is probable that these degenerative processes began with the fungal ancestor and not since lichen evolution; it is, however, very likely that the symbiotic associations hasten the retrogressive changes as far as the apothecia and spores are concerned, since these are probably of little value in the processes of reproduction. The process of gelatinization begins quite early in the development of the apothecia and reaches its climax at an early period; as a rule spores are few in number, while the apothecia occur quite plentifully.

The *Verrucarias* as above limited seem to be quite cosmopolitan; their usual habitat is rock. The majority of so-called tree *Verrucarias* belong to other genera.

PLATE 56.

VERRUCARIA RUPESTRIS Schrad.

1. Natural size.
2. Apothecium and portion of thallus magnified.
3. Section of apothecium.
4. Section of thallus.
5. Galatinous paraphyses and spore-sac.
6. Spores. a, simple forms; b, septate forms.
7. Hyphae and algae (*Pleurococcus vulgaris*.)

7. PERTUSARIA DC. Fl. Franc. 2: 319. 1895.

This group is usually placed near *Urceolaria* among the Parmeline lichens. There is, however, no reason why it should be given such a position; the apothecial characters indicate the true relationship which is doubtless with the Verrucariaceae, close to *Trypethelium* and *Pyrenula*. It is affirmed that some *Pertusarias* have apothecia resembling those of *Lecanora*, thus indicating a relationship to the Parmeliaceae; such a resemblance seems to exist in the higher European forms of this genus. In all the species which came to my notice from our territory the apothecia are globose and immersed either in the substratum or in the thallus. The close relationship to *Trypethelium* is very apparent from a critical study of *P. pustulata* which is one of the lowest representatives of the genus; in this species the thallus and apothecia are almost entirely hypophloeodal, the latter occurring in clusters forming warty elevations of the bark; the apothecia open by very minute, almost imperceptible pores. In the majority of *Pertusarias*, however, the thallus inclusive of apothecia is epilithic or epiphloeodal. To these the following general description applies.

The thallus is essentially crustaceous in its general appearance; there is, however, a fairly well developed upper cortical layer; the medullary tissue is also well developed; no lower cortical layer is present, the entire thallus being closely adnate to the substratum by means of the numerous rhizoidal hyphae; the upper surface is almost smooth, warty to papillose; the thallus is quite variable in thickness and in the higher European forms the thallus becomes

more or less lobate. The color varies from light grey to greenish grey. The algae (*Cystococcus humicola*) are normal in appearance and do not seem to occur very plentifully.

The apothecia are minute, globose and emersed in the warty elevations where they occur in colonies of five or six. Usually there is no perceptible pore-opening. In the higher forms the part of the thallus above the disk becomes more or less sunken, which to casual observance may give the appearance of an apothecial disk. In the majority of species the apothecium remains globose, being almost entirely enclosed by the usually colorless perithecium.

The paraphyses are long, slender and more or less branched; they are quite gelatinous and perfectly colorless. The spores are mostly very large, simple, colorless and usually one to three in each enormously developed spore-sac. The spore-wall is very thick, and in some species (*P. communis*) the inner membrane is reticulately thickened. During germination hyphae begin to form at the thin areas. The plasmic contents are granular, sometimes bearing oil globules.

The *Pertusarias* are also characterized by the numerous soralia which form upon the upper surface of the thallus, often in rounded masses, almost white in color, which may on casual observation be taken for apothecia; these have been made the subject of special study by Darbishire.[1]

Most of the representatives are cosmopolitan, occurring either upon rock or bark, but some also occur on mosses.

PLATES 57 and 58.

PERTUSARIA COMMUNIS DC.

1. Natural size.
2. Semidiagramatic section of apothecium. a, cortical layer; b, algal layer; d, apical pore through which the spores escape; c, medullary tissue; e, thecium.
3. Section of apothecium.
4. Section of thallus.
5. Paraphyses and spore-sac. a, young spore-sac; b, later stage; c, mature spore-sac with three spores; d, spore-sac with apical segment removed to allow the escape of the spores.
6. Mature spore. a, exosporium; b, endosporium with reticular thickenings as seen in optical section; c, oil globules.

[1] Die deutschen Pertusariaceen mit besonderer Berücksichtigung ihrer Soredienbildung. Engler's bot. Jahrb. **22**: 593-679. 1897.

8. Dermatocarpon Eschw. Syst. Lich. 21. 1824.

This genus, considered from a morphological standpoint, forms the connecting link between *Verrucaria* and *Endocarpon*. Phylogetically it does not seem to be derived from *Verrucaria*, as is indicated by a marked difference in the spore-characters. It is more than likely that these two genera are represented by two different fungal ancestors derived from some generic groups of the Sphaeriaceae.

The description of this genus is based upon the characters occurring in the only well-known representative, namely, *Dermatocarpon pusillum*, usually included in *Endocarpon*.

In *D. pusillum* the thallus, though very minute, is typically foliose. There is present an upper cortical layer, an algal layer, a medullary layer, but no true lower cortical layer, its place being taken by a layer consisting of a more dense network of hyphal tissue whose cell-walls are dark colored. The thallus, consisting of a single entire lobe, is held to the substratum by numerous rhizoids. As a rule, the thalli occur in clusters of five to twenty or more; more rarely they occur isolated over the substratum. The algae (*Pleurococcus vulgaris*) are quite numerous and are arranged in a manner typical of this alga when occurring in the lichen-symbiosis, that is, they occur in vertical more or less irregular rows, closely surrounded by the semi-cortical hyphal tissue.

The apothecia are very small, usually one on each thallus. They are immersed in the thallus opening by an irregular pore in its superimposed tissues (algal layer and upper cortical layer). The hypothecium is dark and shows a tendency to become cortical. The paraphyses are almost entirely gelatinized, as are also the spore-sacs.

The genus is at once recognized by its spore-characters. In *Verrucaria* and the related group, *Endocarpon*, the spores are simple, colorless and eight in each spore-sac, while in *Dermatocarpon* as represented by *D. pusillum* there are from one to three colorless more or less ovoid multilocular spores. It may, however, be possible that there are species of *Dermatocarpon* with eight spores in each spore-sac. Further careful revision of *Verrucaria*, *Staurothele*, *Dermatocarpon* and *Endocarpon* will reveal whether this be so or not and also whether all species of *Dermatocarpon* have foliose thalli.

Another character constantly met with in *D. pusillum* is the presence of thecial algae, which are ejected with the spores to which they adhere (see discussion of Thecial Algae).

D. pusillum is rather difficult to find because of its minuteness. It seems to be southern in its range and rather rare, occurring upon limestone.

PLATE 59.

DERMATOCARPON PUSILLUM (Hedw.)

1. Natural size.
2. Four apothecium-bearing areoles of the thallus, magnified.
3. Section of the apothecium.
4. Section of the thallus.
   a, upper cortical layer; b, algal layer; c, medullary tissue; d, dark colored lower limiting layer; e, rhizoidal hyphae.
5. Paraphyses and spore-sac.
6. Spores with adhering algae (thecial algae).
7. Algae of the thallus.
8. Thecial algae.

9. ENDOCARPON Hedwig, Stirp. Crypt. 2: 56. 1789.

All the characters of this genus indicate its close relationship to *Verrucaria*. It seems still more closely related to *Dermatocarpon*, with the exception of the spore-characters, which are widely different, as already indicated; the high development of the thallus in this genus determines the relatively high position of the family to which it belongs; yet it may be questioned whether the Verrucariaceae should be placed higher than the Parmeliaceae. According to Reinke they take even a higher position than is here accorded them.

The representatives of the genus are distinguished from the species of *Verrucaria* by the presence of a foliose thallus. In the lower *Endocarpons* (*E. hepaticum*) the thallus-lobes are quite small and closely adherent to the substratum, reminding one much of the thallus of *Dermatocarpon pusillum*; in the intermediate forms (*E. fluviatile*) the thallus-lobes are much larger and more or less ascending, while in the highest forms (*E. miniatum*), the lobes are very large and attached by an umbilicus, in fact closely resembling the thallus of some *Umbilicaria* or *Gyrophora*; in consistency the thallus is rigid, being comparatively thick; its color is quite variable; grey and brown seem to be the predominating colors; the lower surface being usually darker than the upper; the dark lower surface of *E. miniatum* usually bears numerous wart-like elevations which upon examination prove to be the apothe-

cia of some parasitic fungus; these apothecia take their origin just above the lower cortical layer; as growth proceeds the cortical layer is pushed outward and finally ruptures, allowing the rather large black apothecia to protrude; the spores of the parasite are oblong, elliptical, colorless, two to four-celled. Most works on lichens refer to the apothecia as "warty outgrowths on the lower surface of the thallus." Further critical study is necessary to find the true morphological and physiological relationship of parasite to host; incidentally it may be mentioned that careful sectioning does not reveal the structural union between host and parasite; also that the same parasite seems to occur constantly, so that the question might arise which are the true apothecia of *Endocarpon miniatum*, or whether both forms of apothecia belong to parasitic fungi.

As already mentioned, the thallus is quite thick; the upper and lower cortical layers are well developed; the algae (*Pleurococcus vulgaris*) are situated in a semicortical tissue just below the upper cortical layer; the algal cells, which are larger and more irregular in shape than those in *Dermatocarpon* or *Verrucaria*, seem to occur within the hyphal cells. No haustoria occur, since none are needed. The products of assimilation pass through the algal and fungal cell-walls by direct osmosis. The medullary hyphae are much branched and comparatively short-celled, forming a rather close mesh-work.

The apothecia are very numerous, small, and wholly immersed in the thallus; they open by minute pores through which the spores escape. The paraphyses, spore-sacs and spores are in all respects similar to those of *Verrucaria*. The representatives of the genus seem to be more or less cosmopolitan, but *E. miniatum* is by far the most common in the territory; they occur upon the soil, rocks and the bark of trees.

PLATE 60.

ENDOCARPON MINIATUM (L.) Schaer.

1. Thallus natural size.
2. Section of apothecium.
3. Section of thallus.
4. Spore-sac with spores.
5. Spores.
6. Algae enclosed by hyphal cells.

Family 8. COLLEMACEAE.

This is without doubt the most clearly defined and natural lichen-family, its representatives being at once recognized by the presence of the alga *Nostoc* (except in the genus *Hydrothyria*). The generic groups doubtless form a continuous series, having no close relationship to generic groups of any other family. According to the spore-characters they are perhaps most closely related to *Psoroma* and *Pannaria* of the Pannariaceae.

All of the members of the family are foliose, from the lowest to the highest; the algae are numerous and usually quite uniformly distributed throughout the entire thickness of the thallus. For this reason they were formerly designated as homoiomerous lichens. The highly gelatinous condition of the thallus is due to the gelatinous covering of the algae and not to special gelatinization of the hyphal cell-walls. A cortical layer is present in the forms above *Collema*, but none exists in that genus and it should therefore be compared with crustaceous lichens, at least when considered from the standpoint of comparative morphology. The principal reason why it differs essentially from the usual crustaceous lichens is due to the presence of the algal gelatine which gives the thallus a smooth appearance and does not permit the formation of areoles. In some *Collemas* the thallus-lobes are very small and irregular in form. In all Collemaceae the thallus is considerably folded and rugose, principally due to inequalities in growth and to the interrelation of hyphae and algae. An area of the thallus bearing comparatively more algae than another area of the same thallus will expand more upon the absorption of moisture and cause the two areas to become disturbed relative to each other due to the force exerted. Subsequent processes of growth cause these inequalities to become fixed. (Retardation and acceleration of growth due to pressure.)

In general it may be stated that the morphology of the family indicates a comparatively low stage of development, but their physiological adaptation is highly developed if we consider them from the standpoint of their origin. The algal symbiont, which was originally a form of *Nostoc* closely related to *N. commune*, has undergone great changes by way of adapting itself to new environments; from being dependent upon a constant high degree of moisture it became enabled to exist and thrive upon tree-trunks, rocks, etc.; it also became much reduced in thickness, forming a thin, evenly

spreading layer upon the substratum; its greatest adaptations are perhaps in relation to new habitats. Although the Collemaceae may perhaps not be able to resist such extremes of dryness and temperature as most lichens, yet from the original habits of the predominating symbiont (*Nostoc*) it is evident that the adaptive changes were even greater than in the majority of lichens. The changes are, of course, primarily due to the interaction of both symbionts since the establishment of the lichen phylogeny.

The fungal symbiont is doubtless derived from some group of the Patellariaceae. Whether the family has been developed from one or from several fungal ancestors is questionable. From the study of the genera it seems that two ancestors are, perhaps, represented, one for *Collema*, *Leptogium* and *Mallotium*, and one for *Hydrothyria*. In this family, also, the spores are retrogressive in their development, as is indicated by the absence of coloration and a tendency toward simpler forms, which is shown by the existence of non-septate and thin-walled spores. Soredia are comparatively few, due, no doubt, to the difficulty of enclosing the algal gelatine by the hyphae. Haustoria proper can not be said to exist in the family. The hyphae lie in contact with the algae and pass through the gelatinous substance, which position is sufficient to enable the hyphae to absorb the assimilated food-substances of the algae.

As to the algal symbiont, it presents the general appearance of *N. commune*; the threads are of about the same length; the heterocysts are, perhaps, somewhat fewer in number; several observers have cultivated it in various media, free from its fungal symbiont. The algal symbiont of *Hydrothyria* is *Rivularia*.

As already stated, the members of the Collemaceae are foliose; the color of the thallus and apothecia varies from greyish blue to dark blue. They are attached to the substratum by the gelatine and rhizoids, also by a central attachment, (umbilicus) as in *Umbilicaria*, and are quite common throughout the territory.

KEY TO THE GENERA.

Cortical layers wanting.	1. *Collema.*
Cortical layers present.	
Venation wanting.	
Long rhizoids not present.	2. *Leptogium.*
Long rhizoids present.	3. *Mallotium.*
Venation on lower surface of thallus	4. *Hydrothyria.*

1. Collema Wigg. Prod. Fl. Holst. 89. 1780.

This genus is most typical of the family, and is readily distinguished from the following ones by the absence of a cortical tissue. It is a large genus and further careful study may make a subdivision into two or more genera convenient; the spore-characters seem to make such a division possible.

The general characters not already mentioned in the description of the family are as follows: The thallus consists of numerous minute lobes in the lower forms, while in the higher the thallus-lobes are large and comparatively few; its color varies from dark blue to nearly black; in general the lower surface is somewhat lighter. The resemblance of this thallus to the thalli of other lichens is only apparent; for instance, the thallus of *Parmelia* is also large and lobed, but the histological structure is wholly different, as a comparison will clearly show.

The thallus of *Collema* is perhaps more nearly homoimerous than that of any other lichens, yet it is found that the algae (*Nostoc*) are more numerous near the upper surface. It is evident that the distribution of the algae in the thallus can be of little importance in classification. Of still less consequence is the gelatinous nature of lichens; the algae which give the gelatinous consistency to the thallus are, however, of prime importance. Older lichenologists who introduced the separation into gelatinous and nongelatinous lichens did not recognize the nature of the algae and their relation to the thallus; for that reason such distinctions are no longer of any value in classification.

The apothecia are comparatively small or medium; in some species they are very numerous, in others very few. A thalloid exciple is present which usually extends somewhat above the margin of the thecial disk. The general contour of the apothecium reminds one strongly of the apothecia of *Parmelia* and other related genera. The color of the disk is usually brown to very dark; in form it may be slightly convex, flattened or concave; the margin of the thalloid exciple is frequently crenate. The colorless hypothecium consists of numerous short-celled hyphae. The cells are somewhat rounded and thin-walled; the paraphyses are quite slender and unbranched.

The spore-characters of this group are quite variable; as a rule the spores are colorless, though they may become somewhat colored in some species; they vary from simple (comparatively few) to multi-

locular; the wall and septa are quite thin and translucent or transparent. In general the spores present degenerative characters, indicated by the thin wall, absence of color, and the apparent tendency toward simple nonseptate forms. Frequently the septa become indistinct. In the retrogressive transition-forms from multilocular to transversely septate we find septa formed diagonally to the normal direction (longitudinal and transverse), which are very inconstant in their occurrence.

As already stated elsewhere, the alga of *Collema* has been cultivated in artificial media. It would be interesting to demonstrate whether or not the *Nostoc* of any *Collema* is capable of existing without its fungal symbiont and of leading the life of an independent *Nostoc* without the aid of culture media; also, whether the fungal symbiont is capable of leading an independent existence.

Collemas are propagated vegetatively either by means of soredia or from portions of the thallus. The thallus is also endowed with continuous marginal growth. Each lobe is capable of forming the center of a new individual; it may or may not sever its connection with the mother plant.

The species occur upon bark, mosses, rarely upon rocks, on soil, seldom partially or wholly submerged in water; they are plentiful in the northern and north-temperate zones, both east and west.

PLATE 61.

COLLEMA PULPOSUM Ach.

1. Thallus natural size.
2. Lobe of thallus with apothecia, magnified.
3. Section of apothecium.
4. Section of thallus.
5. Paraphysis and spore-sac.
6. Spores.
7. Algae.

2. LEPTOGIUM Ach.; S. F. Gray, Brit. Pl. 1: 400. 1821.

In all its essential characters this genus closely resembles *Collema*, from which it is no doubt phylogenetically derived. As compared with *Collema*, the thallus-lobes are larger and somewhat more rigid; the rhizoids are comparatively few and slender. The essential difference becomes apparent upon the examination of vertical sections;

in *Leptogium* both the upper and lower cortical tissue is developed, though it is usually one cell-layer in thickness; it is very characteristic, closely resembling in appearance the epidermal layer of a leaf; in certain areas it consists of more than one cell-layer. As in *Collema* the algae are more numerous near the upper surface of the thallus.

The structural differences are more marked in the apothecium; the cortical layer of the thalloid exciple is well developed; the hypothecium is quite thick and cortical in structure.

The spores have the same general characters as in *Collema*; they differ in that they are usually more pointed at the ends; they lie parallel to each other diagonally across the spore-sac, which is also true of *Collema* spores as far as I have been able to observe.

The algal characters are the same as in *Collema*. The habitat of the species and their distribution is the same as in that genus.

PLATE 62.

LEPTOGIUM TREMELLOIDES Fr.

1. Thallus natural size.
2. Portion of thallus-lobe with apothecia, magnified.
3. Section of apothecium.
4. Section of thallus.
5. Paraphysis and spore-sac.
6. Spores.
7. Algae.

3. MALLOTIUM Ach.; S. F. Gray, Brit. Pl. 1: 399. 1821.

Vegetatively this group represents highly evolved forms; it presents a much higher development than *Leptogium*, as is indicated by an increase in the size of the thallus; the cortical layers are also more developed. The algae (*Nostoc*) indicate a marked tendency to accumulate near the upper surface of the thallus. The essential character which distinguishes this genus from *Leptogium* is the presence of numerous long, comparatively rigid, gray rhizoids which extend in clusters from the lower surface of the thallus; they partly serve as organs of adhesion and as special organs for absorbing moisture from the substratum and from the air; incidentally they may also serve as organs of protection by keeping off crawling insects. The bitter lichenic acid which occurs abundantly in these

rhizoids also hinders the attacks of snails which feed upon lichens (Zukal).

As a rule the few representatives which occur in the territory are sterile, while the soredia are very numerous; soredioid or isidioid branches are sometimes common on the upper surface of the thallus (*M. saturninum*); in all probability propagation proceeds from soredia. The apothecia present the general characteristics of those of *Leptogium*; the hypothecium is, however, not cortical; as far as I have been able to observe, it consists of two layers of hyphae the lower of which extends parallel to the surface of the disk.

The habitat and distribution is the same as in *Collema*.

PLATE 63.

MALLOTIUM SATURNINUM (Dcks.).

1. Thallus natural size.
2. Section of apothecium.
3. Section of thallus, with long rhizoids.
4. Paraphyses and spore-sac.
5. Spores.

4. HYDROTHYRIA Russ. Proc. Essex Inst. 1: 188. 1856.

The general macroscopic characters indicate such a close relationship to the foregoing genera of the Collemaceae that one is surprised at the actual histological and physiological differences. Instead of *Nostoc* we find that *Rivularia* is the symbiotic alga, but it may be possible that the original symbiont was *Nostoc*. The changes in the fungal portion, due to the symbiotic association, may have adapted it to become associated with *Rivularia* rather than *Nostoc*; a similar condition of affairs is met with in *Stictina* and *Sticta*. The general morphological characters of the thallus very closely resemble those of *Leptogium* and *Mallotium*. The cortical layers are less clearly marked, in fact, the entire hyphal tissue is semicortical: the outer cortical tissue proper contains no algae: its cells are thin-walled and quite irregular in size, and it usually consists of more than one layer of cells. The lobes of the thallus are quite large and, in color, thickness and consistency, remind one of *Leptogium*: the lower surface is, however, distinctly marked with veins extending from the central point of attachment toward the periphery: in appearance these strongly resemble the venation of a leaf

and they consist structurally of bundles of hyphae extending longitudinally with the long axis of the thallus-lobes just above the lower cortical layer. These are, doubtless, primarily a mechanical tissue adapted to resist longitudinal (pulling) tensions.

The apothecia are comparatively few, scarcely medium in size, and closely resemble those of *Leptogium*. The spores are more elongated and are not multilocular. It seems probable that this is a further degenerative change in the Collemaceous spores. It may, however, be probable that *Hydrothyria* is represented by a different fungal ancestor than the preceding genera.

Another marked peculiarity of *Hydrothyria* is its habitat. Normally it occurs upon rocks in the bottom of clear running water, in which position it matures its spores. Further observations in regard to its life-history are necessary. Its distribution is perhaps much as the preceding genera. Only one species has so far been reported (*H. venosa* Russ.)

It is highly probable that *Hydrothyria* is closely related to *Psoroma* and *Heppia*. For the time being its present position seems to be most nearly in accordance with our knowledge of the subject.

It is also interesting to note that spermagonia have never been observed on *Hydrothyria*, and this seems to be additional evidence that these structures can not be the male reproductive organs, since apothecia are formed without them; they could not occur as parasitic fungi on account of the submerged habit of the plant.

PLATE 64.

HYDROTHYRIA VENOSA Russ.

1. Thallus natural size.
2. Lobe of thallus showing venation on lower surface.
3. Section of apothecium.
4. Section of thallus; d, vein cut transversely.
5. Paraphysis and spore-sac.
6. Spores.
7. Algae.

Family 9. PANNARIACEAE.

The limitations of this family are at present uncertain; certain genera are included which no doubt belong to some other family; *Ephebe*, in particular, is out of place; *Solorina*, *Peltigera* and *Ne-*

phromium are usually classed under a distinct family-group (*Peltigerei*); they have, however, so many characters in common with *Pannaria* and *Physma* on the one hand and *Stictina* and *Sticta* on the other that it seems perfectly justifiable to include them in the family; it is also very difficult to decide upon what characters to base further subdivisions. Upon careful consideration it becomes evident that the characters of the apothecia, of the thallus, or of the algae taken separately will not suffice to establish the family or famlies. For instance, *Pannaria*, *Psoroma*, *Heppia* and *Physma* are closely related according to their spore-characters and the general features of the thallus and apothecium, but differ widely as to the algal symbionts. *Lichina* and *Physma* are closely related by their algae, but differ widely as to the general conformations of the thallus. *Stictina* and *Sticta* are unquestionably closely related, in fact they are quite frequently combined in one genus, yet the algal symbionts are constantly different; from these varying characters it is evident that careful comparative study is necessary to find the true relationships of the genera belonging to the family; it is also evident that constant family characters are not to be found or are at least very few; the algal characters are, perhaps, most reliable; with several exceptions the symbiotic algae belong to the Cyanophyceae, characterized by a blue-green color; in the first five genera the thallus is fruticose (excepting *Lecothecium*); in the remaining genera the thallus is typically foliose and shows some high structural adaptations; the apothecial characters differ considerably and likewise show structural adaptations indicating a higher specialization; since these specializations are quite variable they will be discussed in the generic descriptions in so far as they have not already been described.

The question may be raised why the fruticose types are considered lower in this family and higher in the Parmeliaceae. The fruticose types of the Pannariaceae are small and present a low organization as lichens, while just the reverse is true of the fruticose types of the Parmeliaceae. To solve the relationship of the fruticose to foliose thalli and their relative position in the scale of development as lichens it is necessary to consider the morphology of the algal as well as fungal ancestral forms in so far as that is possible. As already indicated, the morphology of the ancestral forms of the symbionts has a marked influence upon the development of the lichen. This is well illustrated in *Ephebe* and *Lichina*; both are fruticose lichens, though

widely different in their general histology; in the former the algal symbiont forms the general structure, in the latter the fungal symbiont gives form to the thallus.

KEY TO THE GENERA.

Symbiotic algae *Sirosiphon* — 1. *Ephebe.*
Symbiotic algae not *Sirosiphon.*
  Thallus crustaceous, dark. — 2. *Lecothecium.*
  Thallus fruticose, minute.
    Cortical tissue wanting; spores simple.
      Algae *Rivularia.* — 3. *Lichina.*
      Algae *Gloeocapsa.* — 4. *Omphalaria.*
    Cortical tissue present; spores two-celled, colorless. — 5. *Polychidium.*
  Thallus foliose.
    Spores simple, colorless.
      Algae bright green (*Cystococcus*). — 6. *Psoroma.*
      Algae blue-green (*Scytonema*). — 7. *Heppia.*
      Algae blue-green (*Polycoccus*). — 8. *Pannaria.*
    Spores not simple.
      Lower cortical layer wanting.
        Spores 4–6-celled, colorless, acicular. — 9. *Peltigera.*
        Spores 2-celled, brown. — 10. *Solorina.*
      Lower cortical layer present.
        Spores 4-celled, elliptical, colorless. — 11. *Nephromium.*
        Spores 2–4-celled, colorless, acicular.
          Algae blue-green. — 12. *Stictina.*
          Algae bright green. — 13. *Sticta.*

1. EPHEBE Fr. Pl. Homon. 256. 1825.

This genus, which is represented by two species, only one of which has came to my notice, stands without a parallel in the history of lichen-development. Its general structure and appearance is determined by the algal symbiont, which is *Sirosiphon pulvinatus*; it is therefore very small, dark in color and branching. The thallus consists of the alga mentioned, through the interior of which the hyphae extend. The hyphae, which are so few in number as not to materially modify the appearance and form of the alga, extend in a longitudinal direction between the algal cells, usually terminating at a short distance behind the apex; it may happen that some of the

algal branches remain without hyphae. It must also be remembered that careful examination with the aid of a good microscope is absolutely necessary to determine whether the plant under consideration is *Sirosiphon pulvinatus* or *Ephebe pubescens*. The hyphae are furthermore quite slender and devoid of any special characteristics of color and form.

The difficulty is further increased by the fact that apothecia are very rare. So far I have been unable to detect any apothecia in the numerous specimens of *E. pubescens* examined. Spermagonia are, however, very frequently present; these appear as minute glistening pustules on the sides of the thallus, finally opening on the exterior by a minute pore.

This group of lichens is evidently low in the scale of development because there are practically no changes in structure or function as the result of the symbiotic association. The lichen occurs in the same position as the alga and, as already indicated, has practically undergone no change in form.

The apothecia are said to occur within the algal tissue in the older branches; these apothecia-bearing branches are recognized by a knotted swollen appearance, and they remain covered by the algal tissue until maturity, when an opening is formed to allow the escape of spores.

The *Ephebes* occur upon rock and soil in wet places or where there is running or dripping water; their distribution seems to be through the temperate and tropical zones.

PLATE 70.

EPHEBE PUBESCENS Fr.

1. Natural size.
2. Branch of thallus magnified; a, apothecia; b, spermagonia.
3. Section of thallus-branch and a spermagonium.
4. Section through a younger portion of a thallus-branch; c, formation of a new branch.
5. Spore-sac with spores (after Crombie).
6. Spores (after Crombie).
7. Sterigmata.
8. Spermatia.

2. LECOTHECIUM Trev.; Kbr. Syst. Lich. Ger., 398. 1855.

The position of this genus is rather difficult to determine. The

representatives which came to my notice have been included under *Pannaria* as *P. microphylla*, *P. nigra* and others. The algae and spore-characters at once indicate that these species can not be included in *Pannaria* nor are the genera even closely related.

The thallus is crustaceous as to its macroscopical appearance. On making sections it is, however, found that a well-marked upper cortical layer is quite constantly present, which is dark in color, due to a deposit of coloring substance in the cell-walls. The algal layer is also well developed and consists of the alga *Rivularia nitida* with its usual gelatinous covering through which the hyphal cells extend. Haustoria proper are not present; the medullary tissue consists of rather short-celled, somewhat frequently branching hyphae which are continuous below with the dark rhizoidal hyphae.

As indicated, the color of the thallus is dark; this is true of all the species which came to my notice; close examination with a hand lens will reveal the fact that the higher forms tend to become foliose, the thallus consisting of very minute scaly lobules, dark above as well as beneath; these lobules are cortical above and below.

The apothecia are of medium size, sessile or partially immersed in the thallus; the disk is flattened, the epithecium brown to dark; the hypothecium is usually of a brown coloration, sometimes blue-black; the spores are few, variable in size and form, due to the fact that but few attain maturity. When mature they are oblong, colorless and four-celled; it may, however, be possible that they become colored, though none such came to my notice. It need scarcely be stated that a true thalloid exciple is not present.

The few representatives so far as known in this country occur in the north temperate zone and the arctic regions; they seem to live normally upon rock or coarse sandy soil.

PLATE 15, fig. 10.

LECOTHECIUM NIGRUM (Huds.)

Paraphyses and spore-sac with two-celled immature spores.

3. LICHINA Ag. Syn. Alg. Scand. xii. 1817.

This interesting group of lichens has been erroneously placed by various authors, owing to the fact that the histology was not sufficiently known. On account of the dark minute much-branched thallus it has been placed near *Ephebe*; again, because of the more or less

globose terminal apothecia it has been thought to be a near relative to *Sphaerophorus*. Both conjectures are wide of the mark.

The thallus is minute, dark in color, dichotomously branched and very rigid when dry. The greater bulk of the structure consists of the hyphae which extend longitudinally in the central portion of the thallus-branches, but describe a trajectory outward near the sides. The arrangement of the tissues is typically radial. There is no cortical tissue; the hyphal projections and branches nearest the outer surface undergo a change whereby they serve as a protective covering, more especially intended to prevent excessive evaporation of moisture. Next to this incipient tegument lies the algal layer; the algae, which are *Rivularia nitida*, occur in chains lying parallel with the curved or diagonally inclined hyphae; it was impossible to observe whether they extend beyond the surface or not, although this is affirmed by some authors. The hyphae do not form haustoria about the algae; they simply extend through the gelatinous covering or lie in contact with them. There are no algae in the central hyphal portion of the thallus, nor do they extend quite to the apex.

The apothecia are small, globose and terminal, appearing as small nodular enlargements on the ends of the branches. At first the apothecium is entirely enclosed by the terminal portion of the thallus, but finally an apical pore is formed which may increase to a considerable size. The epithecium is dark, of about the same color as the thallus. The paraphyses are long and slender, the spore-sacs cylindrical, with eight colorless simple elliptical spores in one row. The hypothecium is colorless and consists of a hyphal network.

Only a few species are known, which grow upon rocks in moist places; they seems to occur in the temperate and tropical zones as well as in the far north.

PLATE 66.

Lichina confinis (Muell.) Ag.

1. Natural size.
2. Terminal portion of thallus with apothecia, magnified.
3. Section of apothecium.
4. Section of thallus.
5. Paraphyses and spore-sac.
6. Spores.
7. Algae.

4. Omphalaria Dur. et Mont., Orb. Dict. 7: 351. 1849.

Considerable uncertainty exists as to the limitations of this genus, caused by the variability of the apothecial and spore-characters, and to a lesser degree by the changes in the algal symbiont.

In this group the thallus has a decided fruitcose tendency. The lobes become broad and irregularly branched in the higher forms, closely resembling, in external appearances, some of the lower *Collemas*. In the lower forms the thallus is small, sparingly branched, with short nearly cylindrical lobes; these, with their terminal, nearly globose apothecia, closely resemble *Lichina*, from which this group is probably phylogenetically derived.

There is no cortical tissue, not even in the highest forms; the outer thin conglomerate layer consists of shriveled hyphae and dead algal cells, similar to that in *Lichina*; this is followed by the algal layer, which consists of hyphal branches, much interwoven and for the most part extending vertically to the outer surface; the individual algal cells closely resemble those of *Lichina*, so that superficial examination is apt to lead to mistaken conclusions. In *Rivularia* the entire algal chain is enclosed by the gelatinous layer. In the algae of *Omphalaria* each cell is enclosed by a gelatinous layer. From this it is evident that the algae are not *Rivularia nitida*, but some species of *Gloeocapsa*, perhaps *G. polydermatica*, though much larger than the form occurring in *Baeomyces roseus* (hypernutrition). Sometimes it also happens that *Nostoc* occurs in the same thallus with *Gloeocapsa*.

The central portion of the thallus, especially in lower forms, is occupied by the hyphal bundle, which is, however, not sharply demarcated from the algal layer. The hyphal branches extend longitudinally, giving off numerous lateral branches. The color of the thallus is very dark, in fact of about the same color (and consistency) as that of the *Collemas*.

The apothecia are rarely numerous, terminal, globose, often wholly wanting; at the beginning soon becoming more or less cup-shaped. They resemble very closely the apothecia of *Lichina*. Sometimes the hypothecium as well as the greater portion of the thecium is dark in color; again these structures appear colorless. The thecium and upper ends of the paraphyses are always dark in color. The spores also seem to be variable; in the majority of species they seem to be simple, colorless, and elliptical;

again they appear larger, colorless, three to five-septate with thin septa and spore-wall. It is likely that further studies of the group will separate it into several genera; at present I have retained them in the one genus, since only a few representatives occur in the territory. Even if all the undoubted and doubtful *Omphalarias* are grouped together they do not form a large genus. The difficulty of studying the group is increased since the higher *Omphalarias* are frequently or quite constantly sterile.

The species occur in the temperate and arctic zones; they grow upon rocks in much the same localities as the *Lichinas*.

PLATE 67.

OMPHALARIA UMBELLA Tuck.

1. Natural size.
2. Terminal portion of thallus with apothecia, magnified.
3. Section of apothecium.
4. Longitudinal radial section of the thallus.
5. Spore-sac and paraphyses.
6. Spores.
7. Algae and haustoria.
8. Chain of *Nostoc*.

5. POLYCHIDIUM Ach.; S. F. Gray, Brit. Pl. 1: 401. 1821.

This interesting genus is represented by only one species, *P. muscicolum*, quite generally included under *Leptogium*, from which it is, however, essentially different; the casual observer is at once struck by its resemblance to *Ephebe pubescens*; its histology is, however, quite unlike.

The thallus is minute, typically fruticose, consisting of cylindrical branches of a dark color, in fact almost identical with *Ephebe* as far as external appearances are concerned; usually, however, the lobes are shorter.

Upon examining carefully prepared sections the following structure is revealed: there is an outer tissue consisting of one layer, which is typically cortical, very closely resembling the epidermal layer of a leaf in higher plants; the entire interior is occupied by a hyphal tissue and the algae; the algae (*Rivularia nitida*) are most numerous toward the outer surface; the central tissue is, however, never totally devoid of algae; since the thallus is typically fruticose the

structure is, of course, radial, and, as in *Omphalaria*, the algae seem to have undergone considerable change from the normal type.

The apothecia are usually few in number, small, disk-like, sessile upon the basal portion of the thallus, never terminal. The hypothecium is colorless, well developed and typically cortical; the thecium is colorless, the paraphyses rather thick, simple, colorless; the epithecium is light brown; the spores are comparatively large, oblong, elliptical or spindle-shaped, sometimes slightly curved, colorless, two-celled.

It is evident that in its histology *Polychidium* is almost without a parallel. The algae and fruticose structure exclude it from *Leptogium*; the structure and position of the apothecia exclude it from *Lichina* and *Omphalaria*; its resemblance to *Ephebe* is only apparent; it is withal a difficult genus to classify, its present position being only tentative.

As far as known, *P. muscicolum* is rather northern in its distribution, occurring upon rocks and moss in moist places; it has been frequently collected in the mountainous districts of Vermont.

PLATE 68.

POLYCHIDIUM MUSCICOLUM (Sw.) Stein.

1. Plant magnified.
2. Section through apothecium and thallus.
3. Paraphyses and spore-sac.
4. Spores.
5. Algal chain enclosed by the gelatinous covering.

6. PSOROMA Ach.; Michx. Fl. Bor. Am. 2: 321. 1803.

This group differs from the preceding in its algal characters; here the algae are *Cystococcus humicola* instead of *Polycoccus punctiformis*. There is no doubt that *Psoroma* is phylogenetically derived from *Pannaria*; both genera are represented by the same fungal ancestors, as is indicated by the spores, and the apothecial characters. The reason why a given species of *Pannaria* should substitute *Cystococcus* for *Polycoccus* is not known; theoretically the condition of affairs was perhaps as follows: the gradual changes wrought in the ancestral forms of *Pannaria brunnea* finally adapted it to enter into a more suitable symbiotic association with *Cystococcus humicola*, and as a result *Psoroma hypnorum* came into existence;

both lichens now continued to exist side by side, undergoing modifications due to the change of environment. The reason for assuming that in *Psoroma hypnorum* we have a more suitable symbiotic relationship is the fact that this lichen has reached a somewhat higher perfection than *Pannaria brunnea* (compare plates 69 and 71). It may, however, be possible that the hyphae of one and the same lichen may enter into a symbiotic association with either *Cystococcus* or *Polycoccus*. Careful experimentation would decide whether this is possible; some such experiments are highly important, as they would throw light on the permanency or variability of the algal symbiont.

Only two species of *Psoroma* have so far come to my notice from the territory; both have been taken from *Pannaria*; they are *P. hypnorum* and *P. stellata;* they occur upon moss or upon the soil, and seem to be somewhat northern in their distribution.

PLATE 69.

PSOROMA HYPNORUM (Kbr.) Hoffm.

1. Natural size.
2. Section of apothecium.
3. Section of thallus.
4. Paraphyses and spore-sac.
5. Spores.

7. HEPPIA Naeg.; Mass. Geneac. Lich. 8. 1854.

This is a well characterized genus represented by only a few species; or it may be that there is in reality only one species. *H. Despreuxii*, which is the only species so far reported from America, is, in all respects, identical with the European *H. urceolata* and *H. adglutinata*. The following generical characters are, therefore, based upon the study of *H. Despreuxii*.

The thallus is of medium size, typically foliose, but closely adnate to the substratum by means of numerous rhizoids; it is distinctly lobate at the margin; the structure of the thallus is peculiar, being almost entirely cortical throughout, the cells extending vertically; there is a thin layer above and below in which the cells are not elongated vertically, and these layers seem to be identical with the cortical layers of other foliose lichens; there is no medullary tissue proper. Almost the entire space between the thin cortical layers

is occupied by the alga-bearing tissue; the alga in this case is a species of *Scytonema*; its branching, and relative position of the cells are difficult to observe even in the most careful sectioning; they seem to have undergone considerable modification in structure since their association as lichens, and for this reason it is also difficult to determine the species. In the thallus the algal chains extend vertically parallel with the hyphal cells; at certain points they approach very near the upper surface. The color of the thallus is brown above as well as below, becoming quite dark with age.

The apothecia are comparatively large, situated in depressions of the thallus. The apothecium itself is disk-like, but not raised above the general surface of the thallus; there is, therefore, no noticeable line of demarcation between the thallus and apothecium; one passes into the other without any structural differences observable by the naked eye. The hypothecium is colorless and cortical in structure. The thecium is brown, much as in *Psoroma*. The paraphyses and spore-sacs are rather long and colorless; the spores are colorless, simple, thin-walled with somewhat granular contents and quite variable in size and form.

H. Despreuxii seems to be southern in its distribution, though it extends well into the territory. It occurs upon the soil, somtimes upon coarse sand.

PLATE 70.

HEPPIA DESPREUXII (Mont.) Tuck.

1. Thallus natural size; a, apothecia.
2. Section of apothecium.
3. Section of thallus.
4. Paraphyses and spore-sac.
5. Spores.
6. Algae and hyphae.

8. PANNARIA Delis.; Kbr. Syst. Lich. Ger. 105. 1855.

This is another much confused genus, the confusion primarily caused by failure to distinguish or recognize the proper algae.

The thallus is quite distinctly foliose in the majority of species, though the lobules are usually small. In the lower species the thallus presents a crustaceous appearance, but upon careful examination it is found, however, that both upper and lower cortical layers

are present. The crustaceous appearance is frequently emphasized by the presence of numerous soredia or isidioid outgrowths from the upper surface.

The upper cortical layer is well developed, the cells rather large, irregular in form and position. The algal layer is also well developed, the algae being in all cases colonies of *Polycoccus punctiformis* of a bright blue-green color and enclosed by a common gelatinous covering. The medullary layer consists of rather thick rigid branching hyphae, quite frequently becoming somewhat cortical throughout. The lower cortical layer is thinner than the upper and bears numerous long simple usually black rhizoids. The upper surface of the thallus is usually a reddish brown; the lower surface is lighter in color.

The apothecia are rather small, disk-like, sessile upon the thallus, the disk flattened with the thalloid exciple slightly raised. They are numerous in the lower forms, few or wanting in the higher species (*P. lepidota*). The epithecium is reddish brown; thecium and hypothecium colorless, though the latter may be more or less tinged with brown; the spore-sacs are cylindrical with eight colorless simple spores with pointed ends; the exosporium is gelatinous and usually of an irregular outline.

I have excluded *P. lanuginosa* from the genus (see Pseudolichenes); also *P. molybdea*, which does not possess a single character in common with the *Pannarias* proper. There are, no doubt, other so-called *Pannarias* which should also be excluded.

As here limited, the genus seems to be southern, extending, however, well into the north temperate zone, even into the arctic; the species occur upon moss, soil, rocks and trees. *P. brunnea* and a few other species are frequently found spreading over *Polychidium muscicolum* when this lichen occurs on moss. Both lichens seem to thrive well, which makes it probable that we have here a form of mutualism.

PLATE 71.

PANNARIA LURIDA (Mont.).

1. Natural size; a, apothecia.
2. Section of apothecium.
3. Section of thallus.
4. Paraphysis and spore-sac.

5. Spores; a, gelatinous exosporium.

6. Algae; a, impoverished chain from the upper portion of thallus; b, normal free chain; c and d, colonies of algae enclosed by the common covering or membrane.

9. Peltigera Willd. Fl. Berol. 347. 1787.

Although the representatives of this genus are distinctly foliose, yet they have characters not occurring in the great majority of foliose lichens heretofore discussed. One of these characteristic features is the total absence of the lower cortical layer; there is not even any indication of a line of demarcation between the medullary layer and the rhizoidal structure. The thallus itself is large, comparatively thick and rigid, but not brittle, as in *Collema;* it is typically dorsiventral in structure and lies flat upon the substratum, to which it is rather loosely attached; it is simple, with marginal lobes upon which the apothecia are borne; the color above is blue-green which changes to brown; the lower surface is light brown.

The structural features are clearly defined; the upper cortical layer is well developed; its surface is roughened by numerous short hyphae which are structurally and functionally comparable to certain trichomes of higher plants; they also serve to retain the soredia of *Peltigera* and other lichens (*Stictinas*) where these develop into warty structures (*P. aphthosa*). These trichomatic hyphal cells differ from the hyphae of the medullary layer in the greater thickness of their walls and the shortness of the cells. The cells of the cortical layer are closely united, the lumina large, the walls firm and non-gelatinous.

The algal layer is well developed, indicating a high assimilative function; the algae are *Polycoccus punctiformis;* the colonies are small and the chains scarcely discernible; the individual cells are considerably larger than the normal.

The medullary layer consists of a rather loose network of hyphae as in the majority of lichens; it usually contains a large quantity of air; below the medullary layer is another hyphal layer in which the majority of the hyphae extend horizontally in the direction of growth; the cells of this layer are larger and walls thicker than in the medullary layer; it contains but little air, and it no doubt forms a mechanical as well as a protective tissue. An additional mechanical support is furnished by the numerous hyphal bundles occurring

in association with the layer just described; these consist of parallel hyphae extending in the direction of growth and are comparable to the "veins" in the lower surface of the thallus of *Hydrothyria venosa*.

The apothecia are large, orbicular and occur on the margin of the thallus-lobes. They are immersed in the thallus so that the large flat disk is scarcely raised above the surface. This is a marked contrast to the apothecia of the *Parmelias* and the majority of foliose lichens, reminding one somewhat of the apothecia of *Heppia*. The epithecium and upper ends of the paraphyses are brown; the hypothecium is colorless and non-cortical in structure, nor is it separable into layers. The paraphyses are colorless and simple. The spore-sacs are of medium size, cylindrical, with the upper portion of the cell-wall considerably gelatinized; at the upper end occurs a projecting cone of firm lichen cellulose to which the ends of the spores adhere.

The spores are acicular, colorless and three to five-septate, usually slightly curved.

The range of the species is northern, though some of them extend far south. A large per cent. of the known species occur in the territory, particularly in the mountainous regions; they grow most commonly upon moss, but also upon soil, rocks and trees.

PLATE 72.

PELTIGERA CANINA (L.) Hoffm.

1. Plant natural size.
2. Section of apothecium.
3. Section of thallus.
4. Paraphysis and spore-sac.
5. Spores.

10. SOLORINA Ach. Lich. Univ. 27. 1810.

This group, which is represented by only a few species, is very interesting from several standpoints. It resembles the preceding genus in the total absence of a lower cortical layer and in its apothecial characters, but in other respects it is markedly different.

As a rule the thallus is considerably smaller than in *Peltigera*, but is, however, thicker, and shows higher structural differentiations, as we shall presently see; it is loosely attached to the substratum

by means of long rhizoids; the margin is lobed but not so distinctly as in *Peltigera*. The color of the upper surface is brown; the lower surface is a light brown (*S. saccata*), or nearly brick-red (*S. crocea*).

The upper cortical layer is smooth above, that is, no trichomatic hyphae are present. This layer is not of uniform thickness; at certain elongated areas the algae extend almost to the surface, and at these areas the cortical tissue is deficient and the intercellular breathing pores are very numerous. In a vertical section the lower outline of the cortical layer presents a serrate appearance. The algal layer is well developed and is peculiar in that two species of algae are quite constantly present. The predominating species which occurs nearest the cortical layer is *Dactylococcus infusionum*; these algae are most numerous at the above mentioned thin areas. The second species, which is far less abundant, and which occurs just below the former, is, perhaps, a species of *Polycoccus* related to the one found in *Peltigera*; it occurs in groups distributed through the medulla and never intermingles with the other form. It is also noticable that in those areas where *Polycoccus* is quite plentiful, *D. infusionum* is deficient.

It seems probable that this group of lichens is now in a transition stage; that is, it may be assumed theoretically that the original alga was *Polycoccus* and that the phylogenetic modifications in the fungal symbiont are gradually adapting it to enter into a more suitable symbiotic relationship with *D. infusionum*; or it may be possible that the lichen originally entered into a symbiotic association with two species of algae.

The medullary layer very closely resembles that of *Peltigera;* the lower hyphal layer is more highly developed; the hyphal bundles are more numerous and well developed. The reddish color of the lower surface of the thallus is due to a deposit of acid crystals upon the cell-walls of the lower non-cortical limiting layer and the hyphal bundles.

The general characters of the apothecia resemble those of *Peltigera*; as a rule they are, however, not marginal but occur toward the middle of the thallus or its lobe; In *S. saccata* they occur in depressions of the thallus, much as in *Heppia*. The epithecium is dark brown, but in all other respects the apothecial characters closely resemble those of *Peltigera*. The spore-characters are, however,

essentially different; in *Solorina* the spores are elliptical, two-celled, and brown in color. Owing to these marked differences in the spores we can not assume that *Solorina* is derived from *Peltigera* or *vice versa*.

The species are essentially northern in their habitat; they occur upon moss, rock and soil.

PLATE 73.

SOLORINA CROCEA (L.) Ach.

1. Portion of thallus, natural size.
2. Section of apothecium.
3. Section of thallus.
4. Spore-sac and paraphyses.
5. Spores.
6. Algae (*Dactylococcus infusionum*).
7. Algae (*Polycoccus*).

11. NEPHROMIUM Ach. Lich. Univ. 101. 1810.

The representatives of this genus are at once recognized by the fact that the apothecia occur on the lower surface of the thallus.

The general appearance of the thallus reminds one of *Solorina* and *Peltigera;* it is, however, somewhat more lobulate and more rolled in and folded; the upper surface is sometimes rugose; in thickness and consistency it closely resembles that of *Peltigera*.

Upon microscopical examination we find a well developed upper cortical layer without trichomatic hyphae; the algal layer is well defined; in by far the majority of species the alga is *Polycoccus punctiformis*, thus indicating a relationship to *Peltigera*. Authors, however, disagree as to the symbiotic alga; some give *Dactylococcus infusionum*. I find this alga only in *N. arcticum*, which should, therefore, be excluded from *Nephromium* and classified under the genus *Nephroma;* for the time being I have, however, refrained from reëstablishing this genus. If, after a careful study of these groups, it is found that these algal differences apply to a number of species, it will no doubt be advisable to separate them.

The medullary layer is well developed and closely similar to that of *Peltigera;* there is a distinct lower cortical layer, from the lower surface of which the rhizoids extend. As a rule the lower cortical layer is much thinner than the upper part but essentially the same in structure.

The apothecia are borne on the margin of the lower surface of the lobes; they are quite large, orbicular or transversely oval; there is a line of demarcation between thallus and apothecium which consists of a slight ridge of semi-cortical tissue gradually merging into the lower cortical tissue and the thecium. Although the apothecia are developed on the lower surface of the thallus, the disk is turned upward 100° or more by a folding back of the lobe of the thallus; this movement is slowly brought about by a more rapid development of the lower cortical tissue in the immediate vicinity of the apothecium. The general characters of epithecium, thecium and hypothecium are the same as in *Peltigera*.

The spores are spindle-shaped, almost acicular in some species, tinged with a brown coloration and two to six-celled.

The range and habitat of the *Nephromiums* seems to be about the same as that of the *Peltigeras*.

PLATE 74.

NEPHROMIUM LAEVIGATUM Ach.

1. Natural size; a, apothecia on upturned lobes of thallus.
2. Section of apothecium.
3. Section of thallus.
4. Paraphyses and spore-sac.
5. Spores.
6. Spores of *Nephroma arcticum*.
7. Algae (*Dactylococcus infusionum*) of *N. arcticum*.
8. Algae (*Polycoccus punctiformis*) enclosed by hyphae.
9. Free cells of 8 at a, colony at b.

12. STICTINA Nyl. Flora, **43**: 65–66. 1860.

Many authors combine this genus with *Sticta*, since the general structural characters are the same in both genera, but the constant algal differences make it more consistent to keep them separate. It is in all respects a condition similar to that of *Psoroma* and *Pannaria*; that is, *Stictina* represents the oldest type from which *Sticta* branched off by a process of special algal adaptation.

The thallus is quite large, typically foliose, of medium thickness, not brittle; lobation is usually quite distinct; there is no marked tendency in the lobes to ascend; they lie quite flat upon the substratum to which they are rather loosely attached by means of long

rhizoids; the color of the upper surface is usually dark brown tinged with bluish-green; frequently the margin is lined with yellowish soredia; the lower surface is either lighter or darker than the upper.

The upper cortical layer is well developed and of quite uniform thickness; the cells are rather small, the cell-walls are comparatively thick; the uppermost layers are colored a dark brown, evidently a protection against excessive illumination; the algae are *Dactylococcus infusionum* and in their arrangement in the thallus strongly remind one of *Peltigera*; the medullary layer consists of the usual network of hyphae; it presents a yellowish appearance owing to a deposit of yellow acid crystals upon the hyphae. It is this deposit of acid crystals which gives the yellowish color to the soredia and the cyphellae; the lower cortical layer is much thinner than the upper and bears numerous long, usually colored, rhizoids below; the lower portion of this layer is also colored; this layer is also broken here and there by the cyphellae, both forms of which are represented.

Stictinas occur only sterile within the territory. The descriptions of apothecia and spores are based upon the examination of South American specimens. Even in southern specimens apothecia are few; they are rather small, disk-like, sessile upon the upper surface of the thallus. It is worthy of note that the thalloid exciple is very deficient for a lichen in which the thallus is evidently so highly organized. In most of the older apothecia the algae have entirely disappeared; the excipular margin rarely extends above the surface of the disk; otherwise it presents the distinctive tissues of the thalloid exciple; that is cortical layer and medullary layer. In the younger apothecia the algal layer or layers are present, however, only toward the periphery. The hypothecium is not cortical, consisting of a close, indistinct network of hyphae, usually of a brownish color; the paraphyses are of medium length, rather rigid, due to the thick cell-walls, the upper ends are colored dark brown, as is also the epithecium. Here and there the thecium bears pillars of a cortical structure, indicating perhaps a tendency to become thalloid in nature.

Considerable confusion exists as to the nature of the spores. In the majority of species examined the spores were spindle-shaped with a tendency to become acicular, colorless, usually two-celled, though some were four-celled, usually colorless, though coloration may at times be marked (brown coloration of the exosporium in *S. crocata*). In most cases the spores have the appearance of being degenerate,

the septa being indistinct and variable as to number and size; they are indefinite in outline as well as in color.

The *Stictinas* are distinctly southern in their range. They occur upon rocks, trees and moss in shaded places.

PLATE 75.

STICTINA CROCATA (Nyl.).

1. Plant natural size; a, apothecia; b and c, soredia.
2. Section of apothecium.
3. Section of thallus.
4. Paraphyses and spore-sac.
5. Spores with indistinct septa.
6. Spores of *S. fuliginosa*.

13. STICTA Schreb. Gen. 2: 768. 1791.

The general structural characters of the *Stictas* are almost identical with those of the *Stictinas*. We shall therefore mention only those characters which are different.

The thallus as a rule is larger and more distinctly lobed; the lobes are broad, rarely becoming narrowed (*S. nitida*); the margin is entire, or lined with orbicular patches of soredia which may also be scattered over the upper surface of thallus, especially along the hyphal ridges. The thallus is sometimes pustulate, similar to *Umbilicaria pustulata*, only the pustules extend downward so that the upper surface presents a series of depressions lined by the hyphal ridges (*S. pulmonaria*); these ridges are formed by hyphal bundles which fre quently branch and again unite, forming a reticular mechanical tissue to prevent the tearing and breaking of the thallus. In the majority of species the upper surface of the thallus is smooth, the necessary mechanical support being supplied by the cortical layers. The prevailing color is grayish green, becoming brown on drying. The lower surface is lined by a cortical layer bearing numerous rhizoids and cyphellae. Large cephalodia occur on *S. Oregana*. A species of *Mucor* is quite frequently parasitic on some species, especially *S. glomulifera* and *S. amplissima*. The coloration in the upper and lower cortical layers is as in *Stictina;* the deposition of acid crystals is much less than in that genus.

The apothecia vary from small to medium and are much more common than in *Stictina;* in fact, their presence is the rule. In

structure they closely resemble those of *Stictina*; the algae are generally present in the exciple; the thecium consists of two layers; the upper layer is formed by a network of hyphae which extend for the most part vertically and contains a quantity of air; the lower layer consists of agglutinate hyphae which extend horizontally. Sometimes the hypothecium is more or less cortical in structure, especially near the periphery.

The spores are mostly spindle-shaped to acicular, colorless, two- to four-celled and, as in *Stictina*, present degenerative characters.

The *Stictas* are much less southern in their range than the *Stictinas*. The majority occur in the temperate zones; some are distinctly northern. They grow upon rocks, moss and trees, to which they are loosely attached.

PLATE 76.

STICTA AMPLISSIMA (Scop.) Mass

1. Small thallus, natural size.
2. Section of apothecium.
3. Section of thallus.
4. Paraphyses and spore-sac.
5. Spores.
6. Algae.

CHAPTER III.

Leprariaceae—Pseudolichenes.

In this group I have temporarily classed those structures whose position among lichens is uncertain, or which are perhaps not true lichens. The principal genera occurring in the territory are *Lepra* and *Amphiloma* ; of the former we have the representative *L. viridis* Schaer., which is common everywhere, occurring on trees, fences, and rocks in moist shaded places; it is usually recognized as *Pleurococcus (Protococcus) vulgaris* ; upon closer examination it is, however, found that it consists of an association of *Pleurococcus* with the hyphal network of some fungus ; the fungal portion never produces apothecia ; it is also found that in some instances the hyphae are almost entirely wanting ; it is, therefore, in all probability, a case of contingent symbiosis (see Contingent Symbiosis). The structural association of the hyphae with the algal cells is less intimate than in true lichens (see Fig. 2, pl. 1). The haustorial branches do not form such a complete covering or network about the algae; in no instance have I noticed that the haustoria penetrate the alga. In some instances *Lepra* develops a growth which to external appearances resembles a typical crustaceous thallus ; it differs, however, in the absence of layer-differentiations ; that is, algae and hyphae are about uniformly intermingled ; it differs also in the fact that its limitations of growth are not so fixed as in the true lichen thallus ; it may spread over areas several yards in diameter, or it may cover the entire side of a large tree-trunk.

As to the origin of the hyphae nothing definite is known at present. In general it is found that they are quite uniform in the structure and size of the hyphal cells ; the filaments are much contorted and twisted, and the new branches are formed very nearly at right angles to the mother-branch. I am unable to state whether these hyphae originate from spores (of fungi or lichens) or whether they are hyphal branches derived from some lichen or fungus growing in the vicinity ; it is known that hyphae may grow to a great length under suitable conditions. Such suitable conditions are no doubt supplied by the algae which furnish the hyphae with an abundance of assimilated food substances, thus enabling them to grow indefinitely ; apothecia are not formed because of this hypernutrition. It is also

unknown whether the hyphae develop apothecia under any circumstances or not; they evidently do not develop them as lichens.

Amphiloma lanuginosum (Ach.), which has been classed as *Pannaria launginosa* by Koerber, is another doubtful structure. E. Fries is the only investigator who is reported to have found apothecia, but the report is, however, so doubtful that no reliance can be placed upon it; all of the European and American specimens which came under my observation showed no trace of an apothecial structure. As compared with *Lepra* it is a much higher structure; it presents essentially the characters of a lichen-thallus; it has a radial growth with definite marginal outline which spreads slowly while the central portion dies away; the entire thallus is very friable, almost mealy in nature; the upper surface is light grey tinged with green; no cortical structure is present; the upper portion of the thallus is soredioid in nature; in fact the entire thallus may be looked upon as a mass of soredia loosely held together by hyphal threads; the lower surface is somewhat smoother, white or light grey and bears numerous darker rhizoids which usually occur in bunches.

As already indicated, the majority of algae occur in the soredioid association. Haustoria, both ectotrophic and endotrophic, are very numerous; the algae, which are undoubtedly *Cystococcus humicola* Näg., are somewhat smaller and paler green than in *Parmelia* and *Physcia*.

Formerly various lichens and parts of lichens were classed under *Pseudolichenes* or *Lichenes imperfecti*. Of these, six generic groups were recognized: *Isidium* Ach., *Variolaria* Ach., *Lepra* Hall., *Pulveraria* Ach., *Spilonema* Ach., *Pyrenothea* Fr. *Isidium* included the peculiar warty and isidioid outgrowths quite frequent on the upper surface of foliose thalli; it also comprised various sterile warty crustaceous lichens. Under *Variolaria* were included sterile forms of *Pertusaria communis*, *P. lactea*, besides other sterile crustaceous lichens of a grey or whitish color, especially those bearing numerous soredia. *Lepra* included the above described true pseudo-lichen *L. viridis* as well as sterile forms of *Placodium* and perhaps *Rinodina*. Under *Pulveraria* were evidently included incipient primary thalli of *Cladonia* as well as sterile forms of *Calicium*, etc. The characters of *Spilonema* are very uncertain, referring, perhaps, to sterile forms of *Graphis*, *Arthonia*, etc. The term *Pyrenothea* referred, no doubt, to low forms of lichens (perhaps old dying plants)

bearing numerous "spermagonia, pycnidia," or perhaps true parasitic fungi.

The Continental Range of the Lichen Genera Occurring in the Northeastern United States.

Lichens are more widely distributed than any other class of the thallophytes. They are enabled to thrive where neither alga or fungus could exist alone. They occur plentifully in the tropics as well as in the extreme northern regions; in the valleys as well as upon the highest mountain peaks. The majority occur at sea level, while some thrive most luxuriantly at high altitudes as *Cladonia*, *Cetraria*, *Umbilicaria*, some species of *Lecanora*, etc.

The following table gives the general continental range of the lichen genera represented in the northeastern United States. Some of the representatives are not sufficiently known to indicate their true range; such are marked with an *. Those given under "territory" are about uniformly distributed throughout the region.

Northern.	Southern.	Eastern.	Western.	Territory.
		Caliciaceae.		
		Mycocalicium.*		
				Coniocybe.*
				Calicium.
		Cyphelium.		Cyphelium.
				Acolium.
Sphaerophorus.				
		Cladoniaceae.		
	Baeomyces.			
Pilophoron.				
Stereocaulon.				
Cladonia.				
Thamnolia.				
		Lecideaceae.		
Biatorella.*				Biatorella.*
				Biatorina.*
				Biatora.
Bilimbia.*				Bilimbia.
	Bacidia.			
				Lecidea.*
				Celidiopsis.*
				Buelliopsis.*
Buellia.				
Catillaria.*		Catillaria.*		
Megalospora.*				
	Lopadium.			
				Gyalecta.
				Psora.
Gyrophora.				
Umbilicaria.				
		Graphidaceae.		
Hazslinskya.*				Hazslinskya.
	Opegrapha.			
	Graphis.			
	Xylographa.			Xylographa.*
	Arthonia.			
	Mycoporum.			
	Arthothelium.			
		Physciaceae.		
			Rinodina.	Rinodina.
			Placodium.	Placodium.
	Pyxine.			Pyxine.*
	Physcia.			Physcia.
	Theloschistes.			
		Parmeliaceae.		
Urceolaria.				
Haematomma.				
				Lecanora.
				Acarospora.
	Speerschneidera		Speerschneidera	
				Parmelia.
Cetraria.				
			Evernia.	
	Ramalina.		Ramalina.	
Alectoria.				
Bryopogon.				

Northern.	Southern.	Eastern.	Western.	Territory.
				Usnea.
		Verrucariaceae.		
	Trypethelium.			
	Pyrenula.			
				Conotrema.
	Thelotrema.			
	Gyrostomum.			
	Verrucaria.*			Verrucaria.
Pertusaria.				Pertusaria.
	Dermatocarpon.			
				Endocarpon.
		Collemaceae.		
				Collema.
				Leptogium.
				Mallotium.
			Hydrothyria.*	Hydrothyria.*
		Pannariaceae.		
				Ephebe.
Lecothecium.				Lecothecium.
				Lichina.
Omphalaia.				Omphalaria.
Polychidium.				
Psoroma.				
	Heppia.			
	Pannaria.			
				Peltigera.
Solorina.				
Nephromium.				Nephromium.
	Stictina.			
	Sticta.	Sctia.		Sticta.

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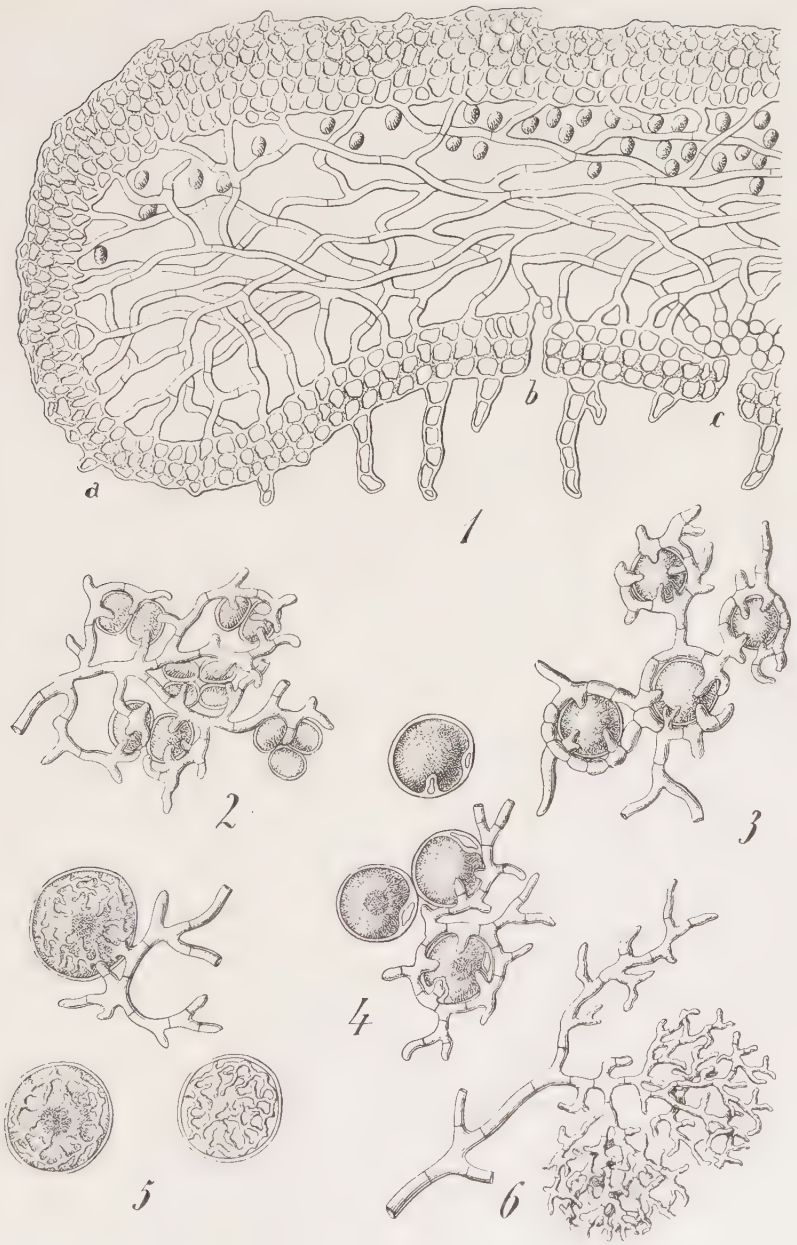
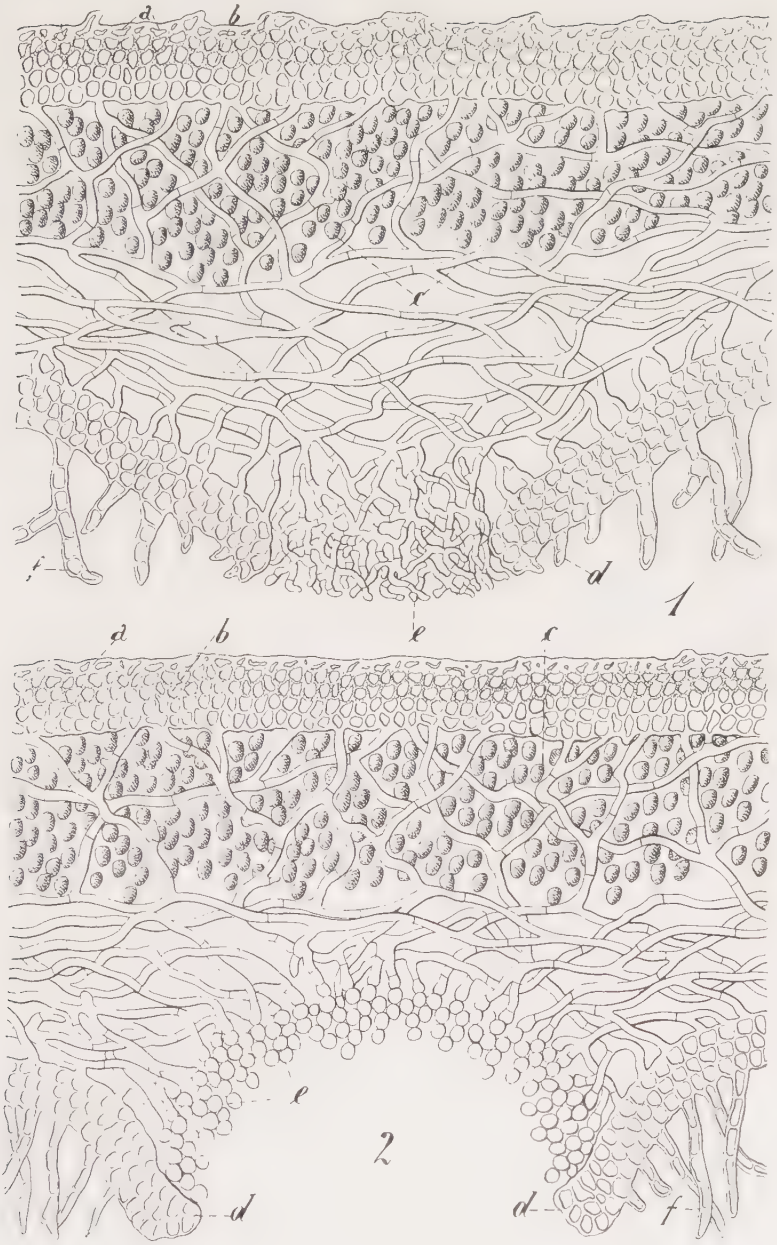


1. APICAL GROWTH AND CYPHELLAE.
2, 3, 4, 5, 6. HAUSTORIA AND ALGAE.



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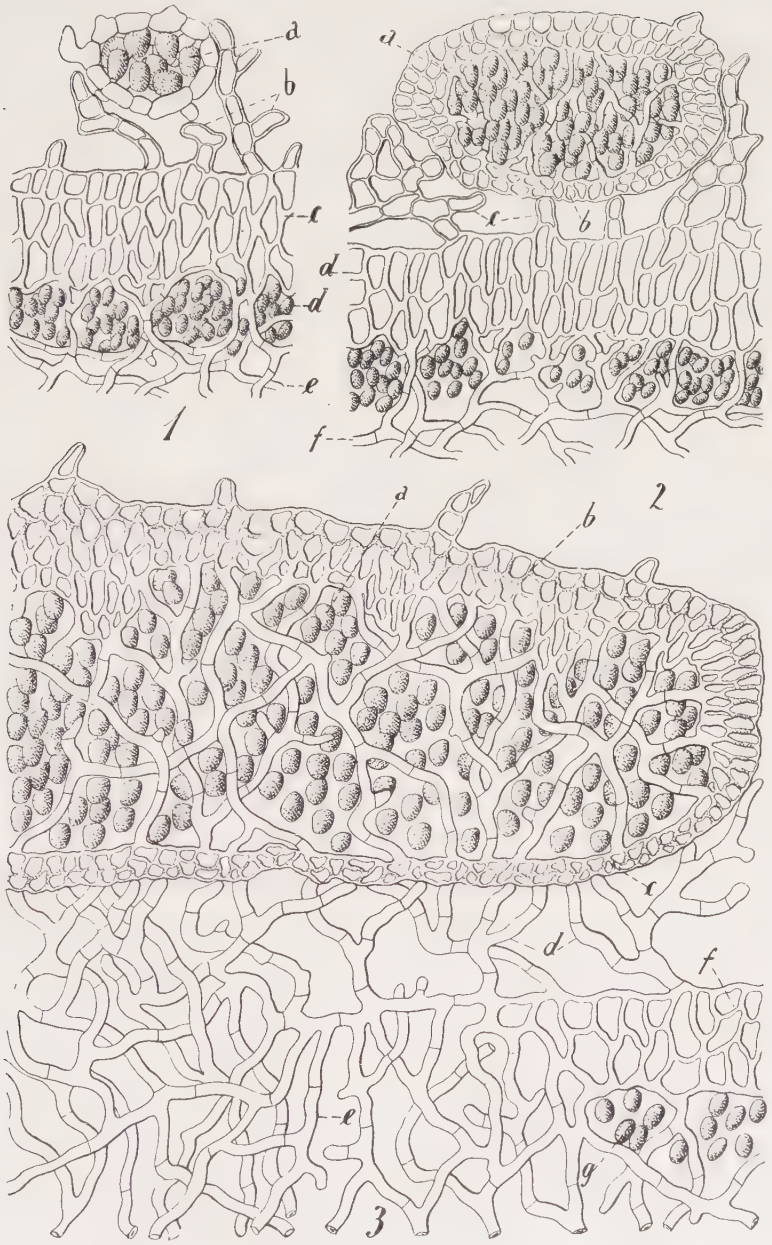

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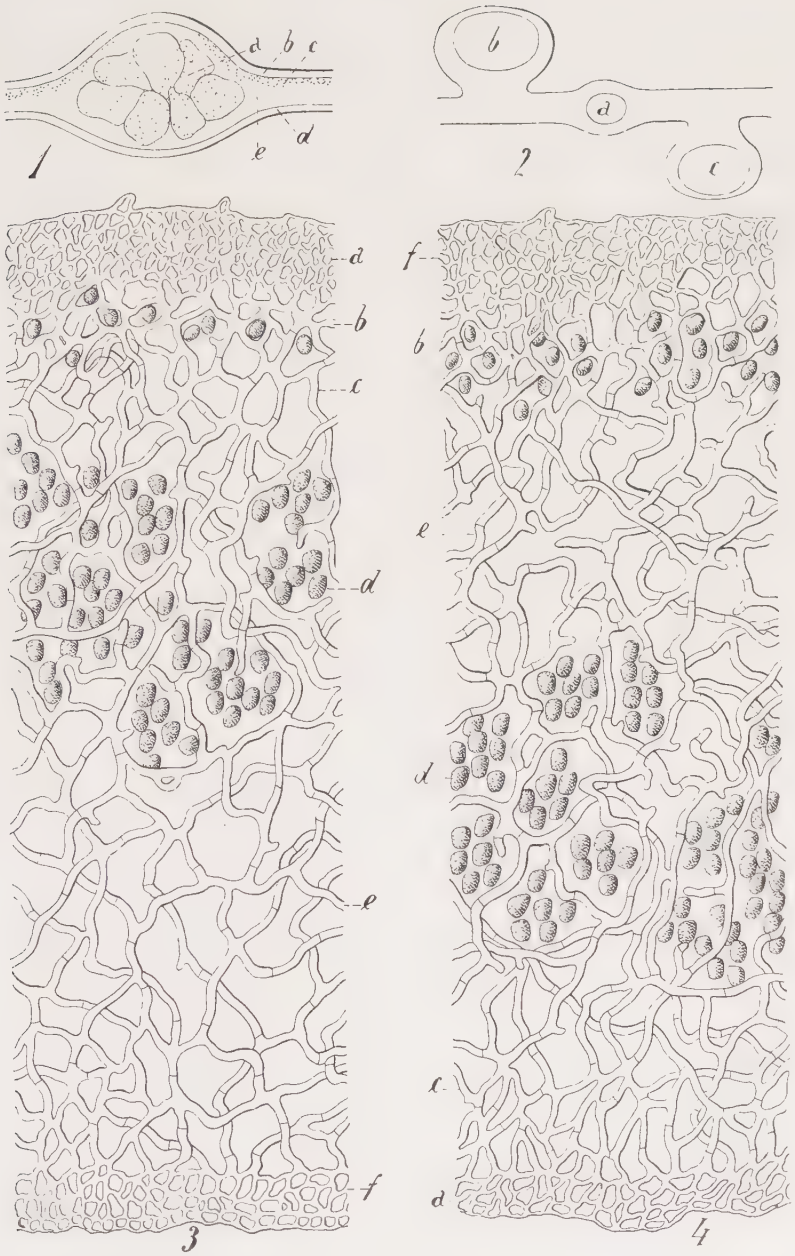
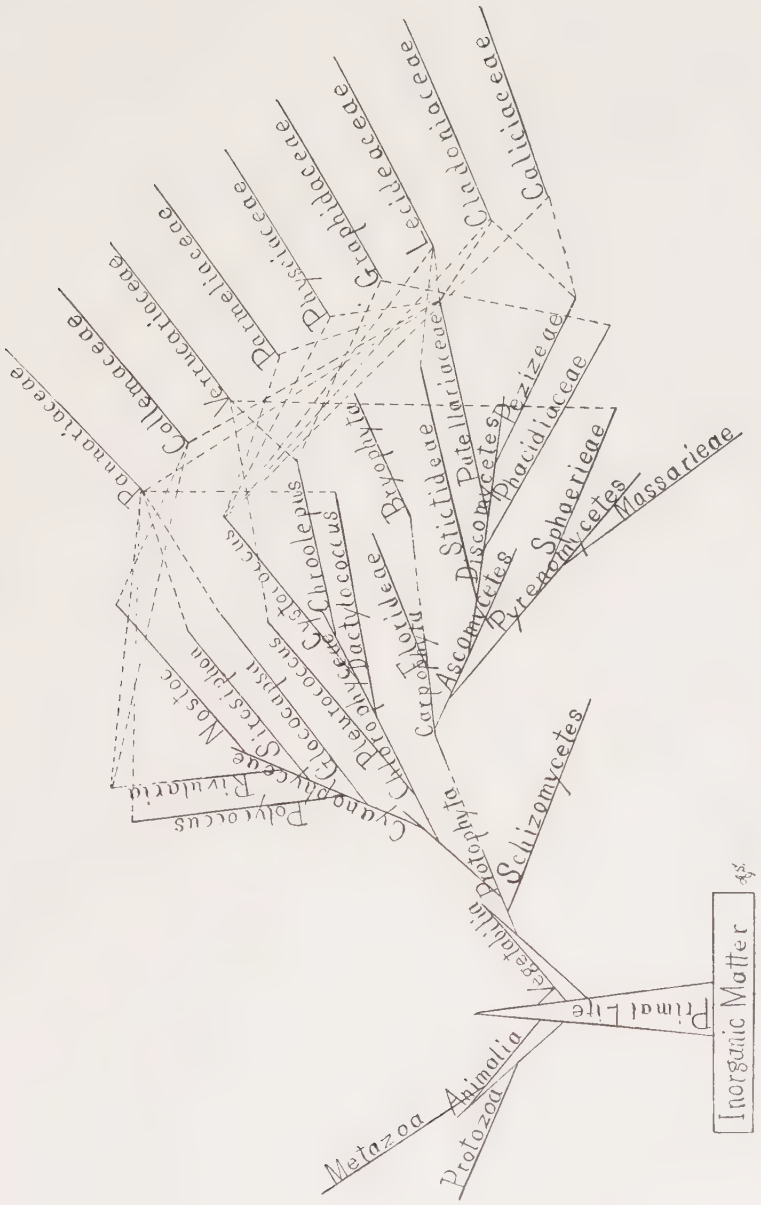


CEPHALODIA OF STICTA OREGANA.


Inorganic Matter
Primal Life
Metazoa
Animalia
Protozoa
Vegetabilia
Protophyta
Schizomycetes
Cyanophyceae
Nostoc
Sirosiphon
Glococapsa
Pleurococcus
Chlorophyceae
Cystococcus
Chroolepus
Dactylococcus
Florideae
Carpophyta
Bryophyta
Stictideae
Pyrenomycetes
Massarieae
Ascomycetes
Discomycetes
Sphaerieae
Phacidiaceae
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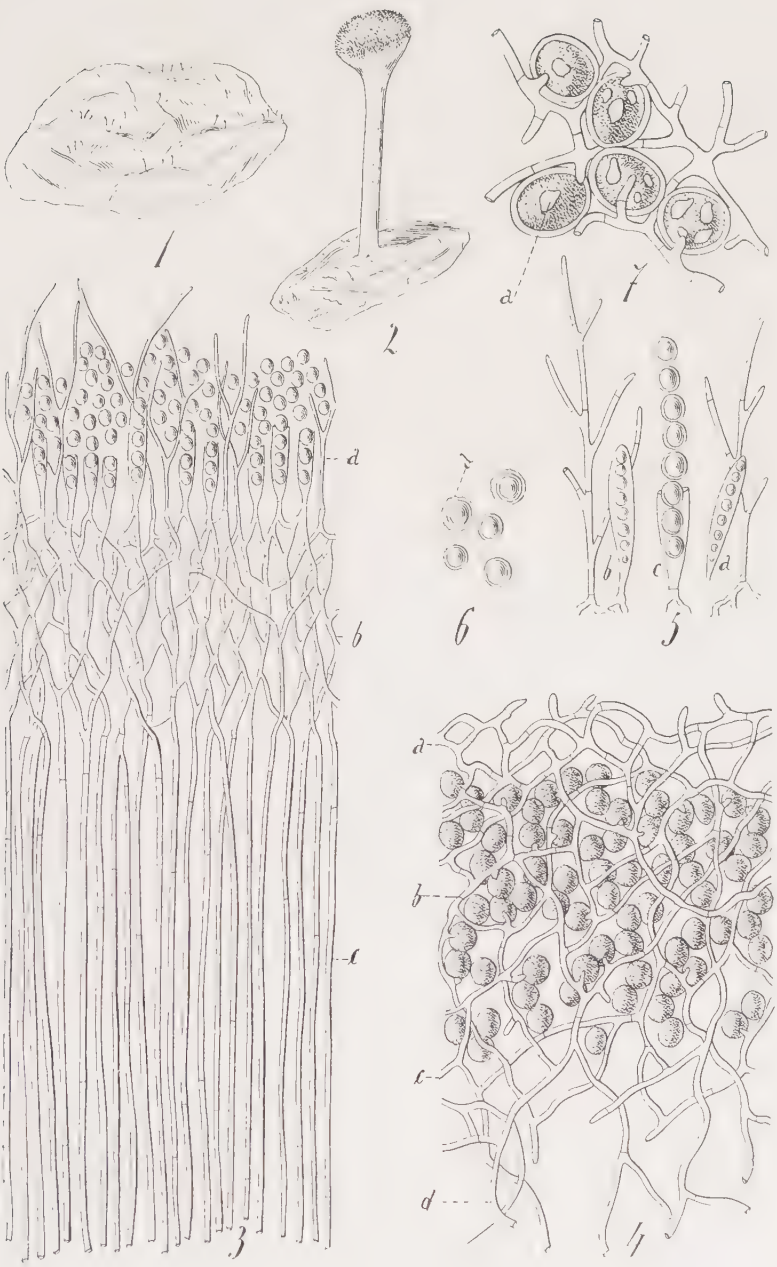
Parmeliaceae
Physciaceae
Graphidaceae
Lecideaceae
Cladoniaceae
Caliciaceae



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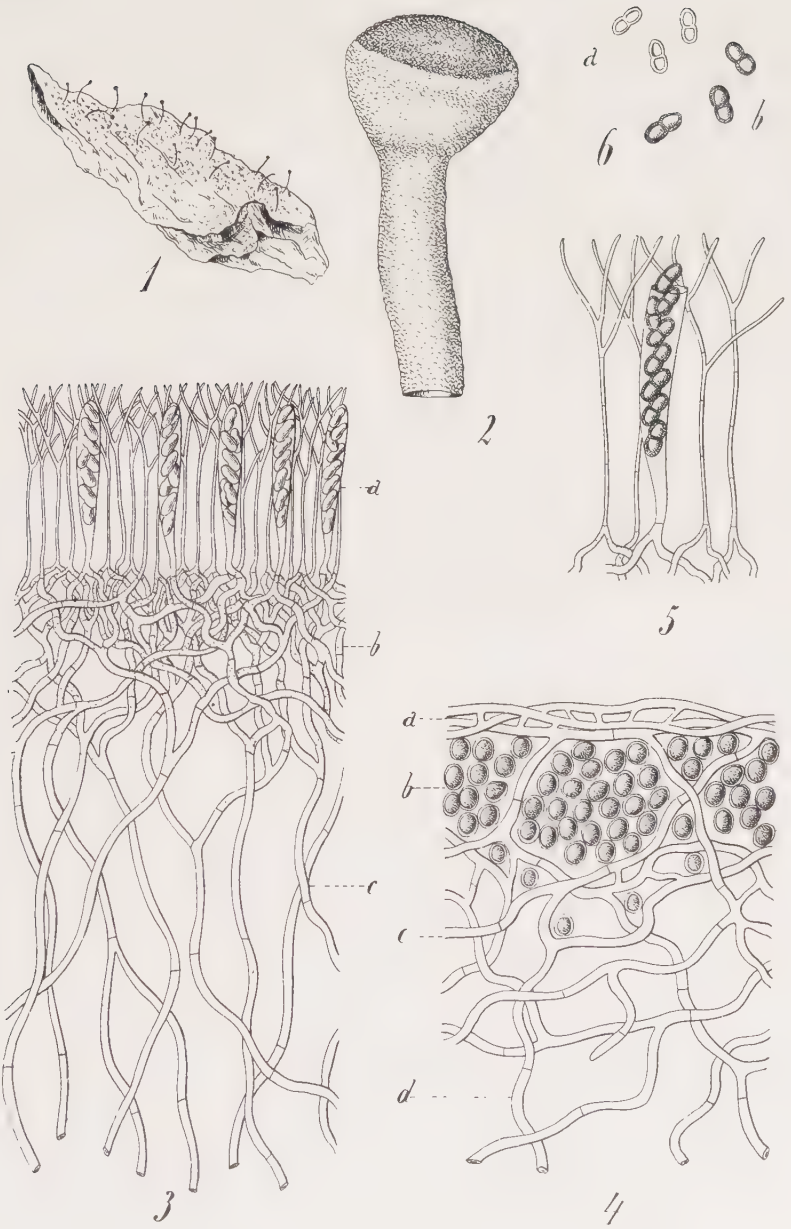
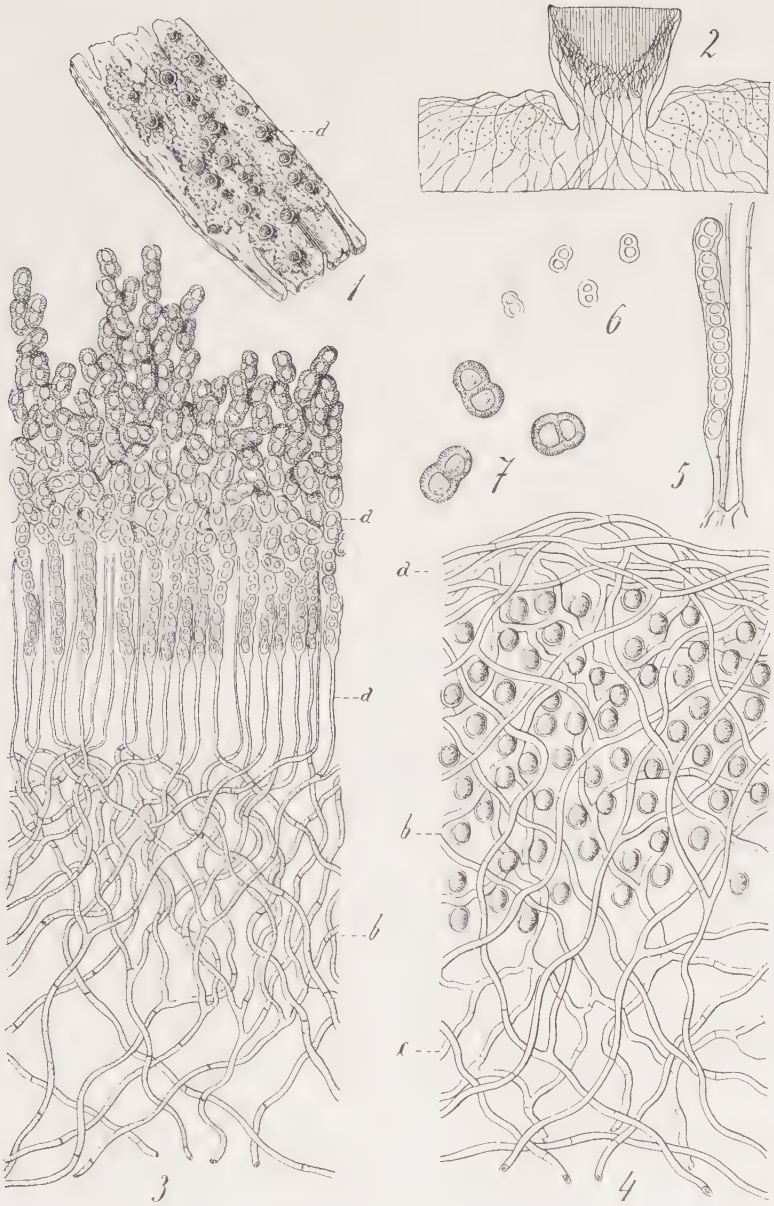


CALICIUM QUERCINUM.



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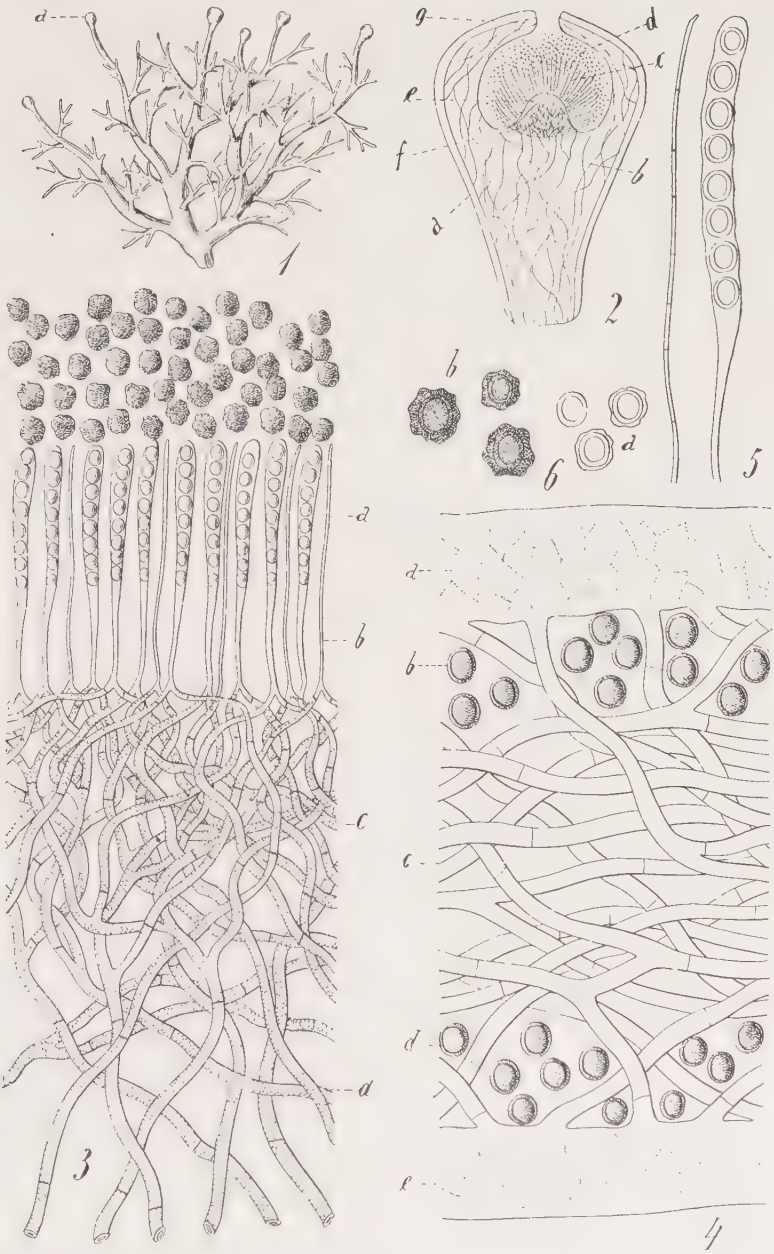

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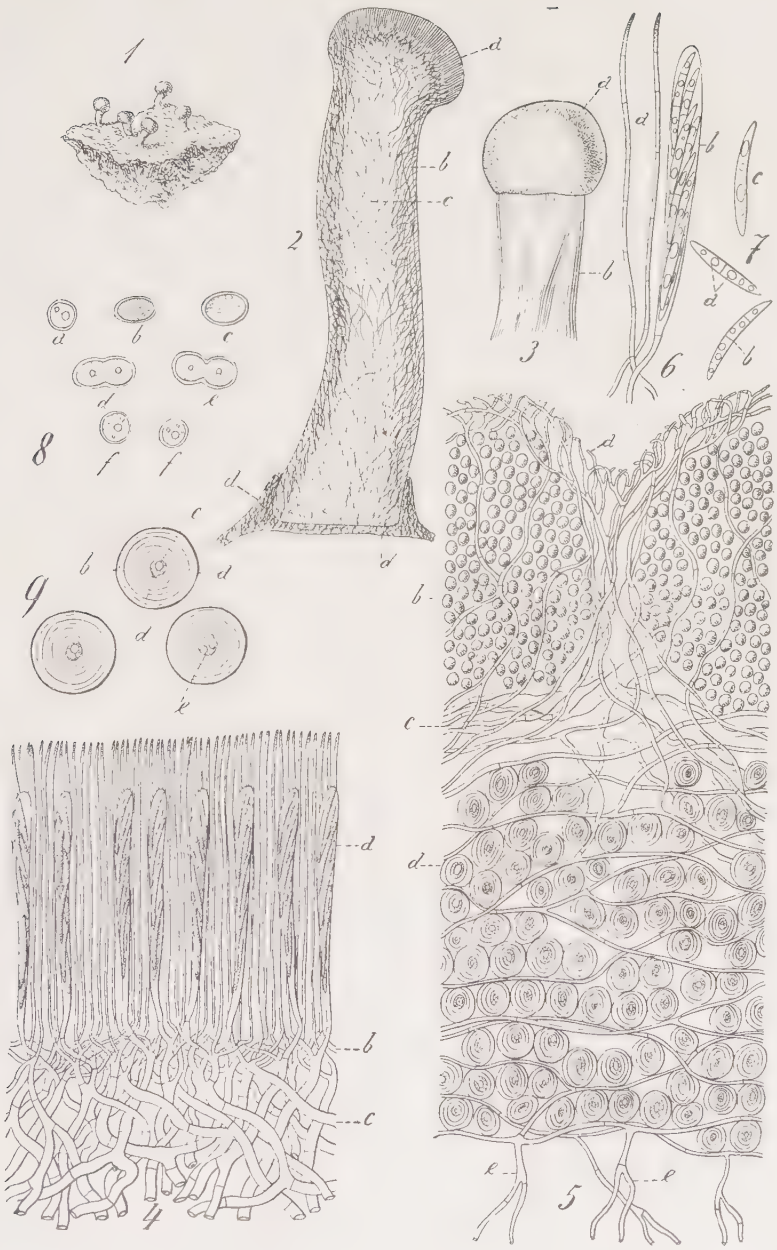

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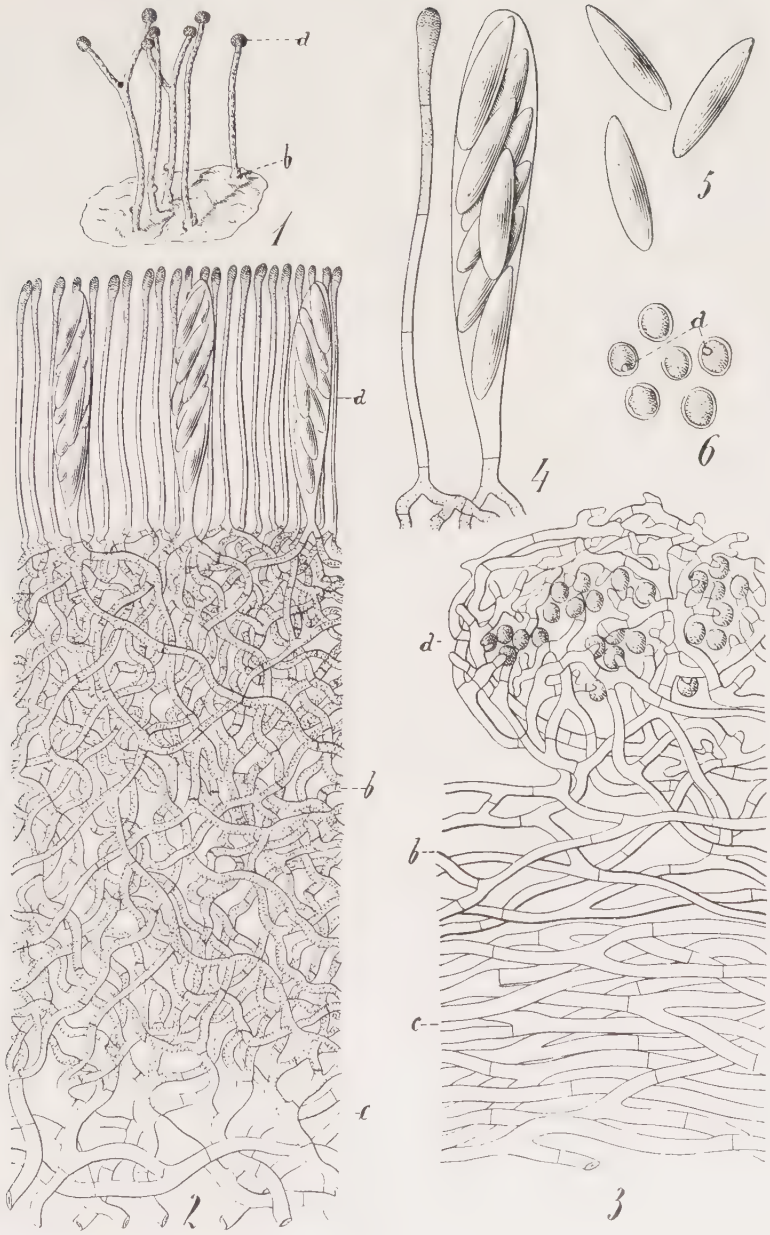

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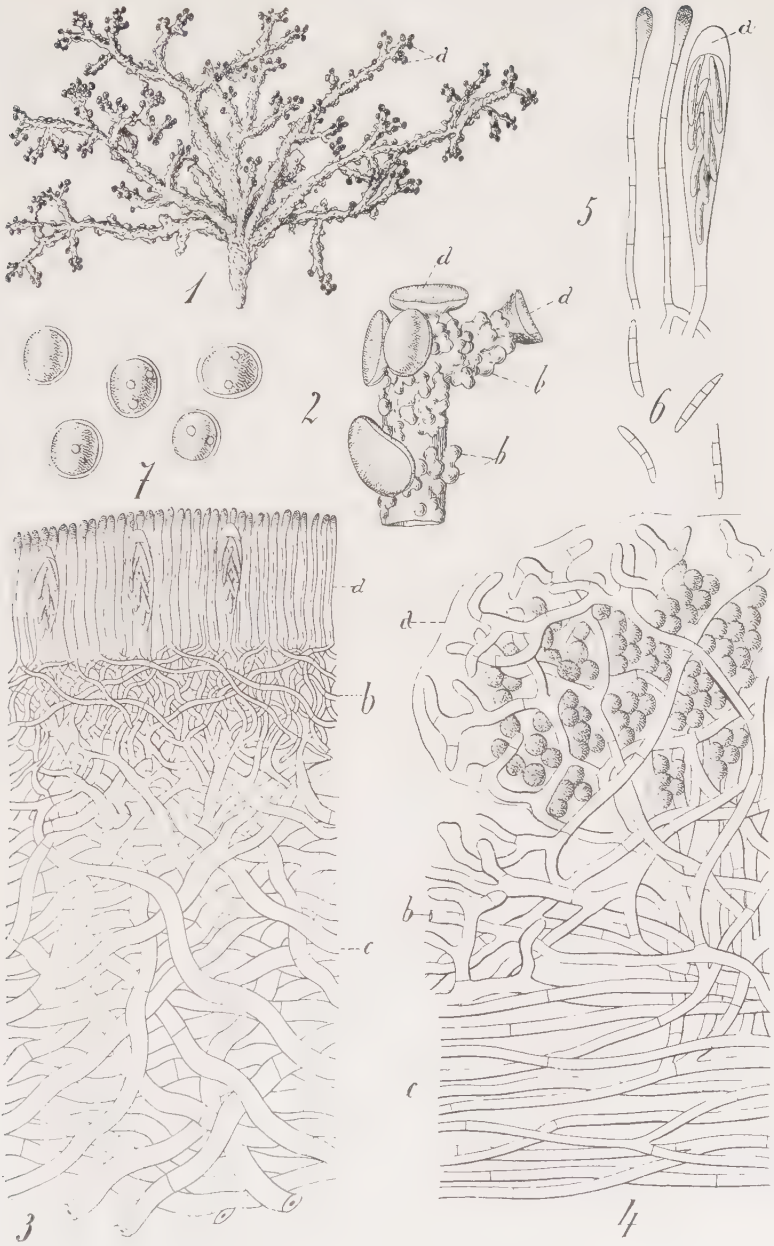

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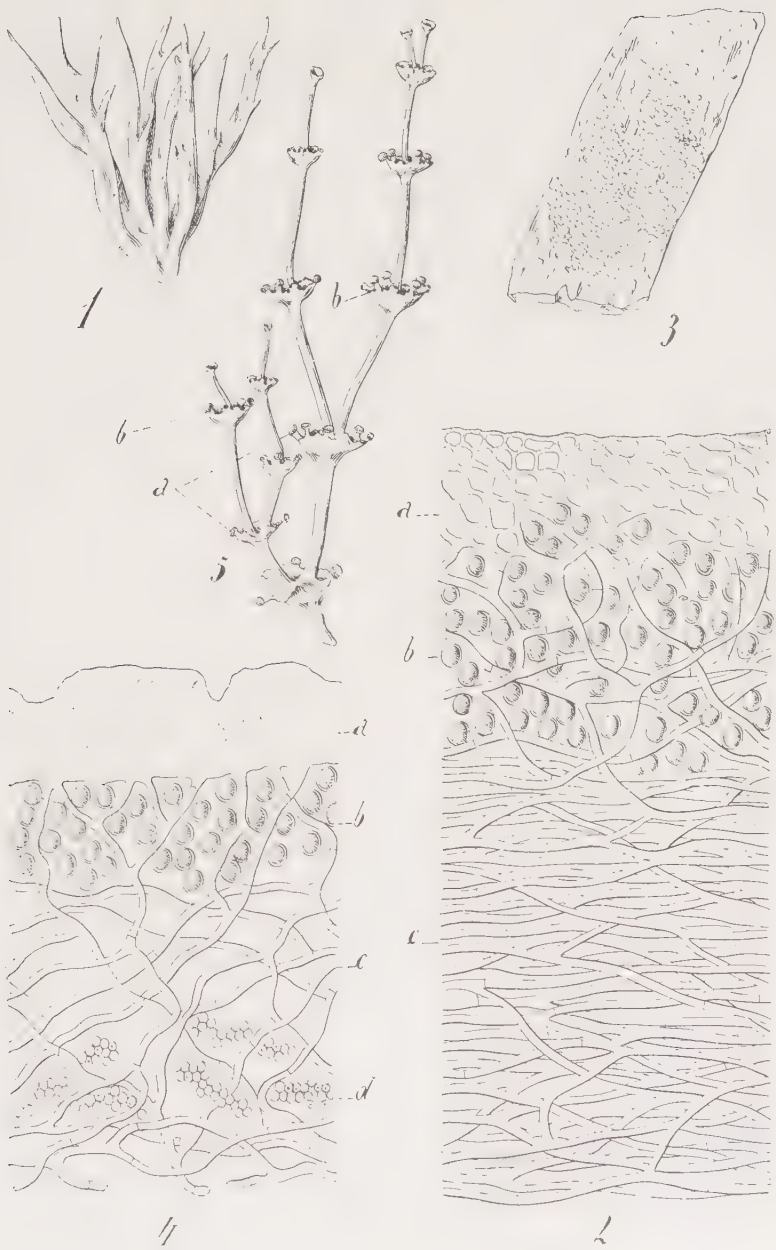

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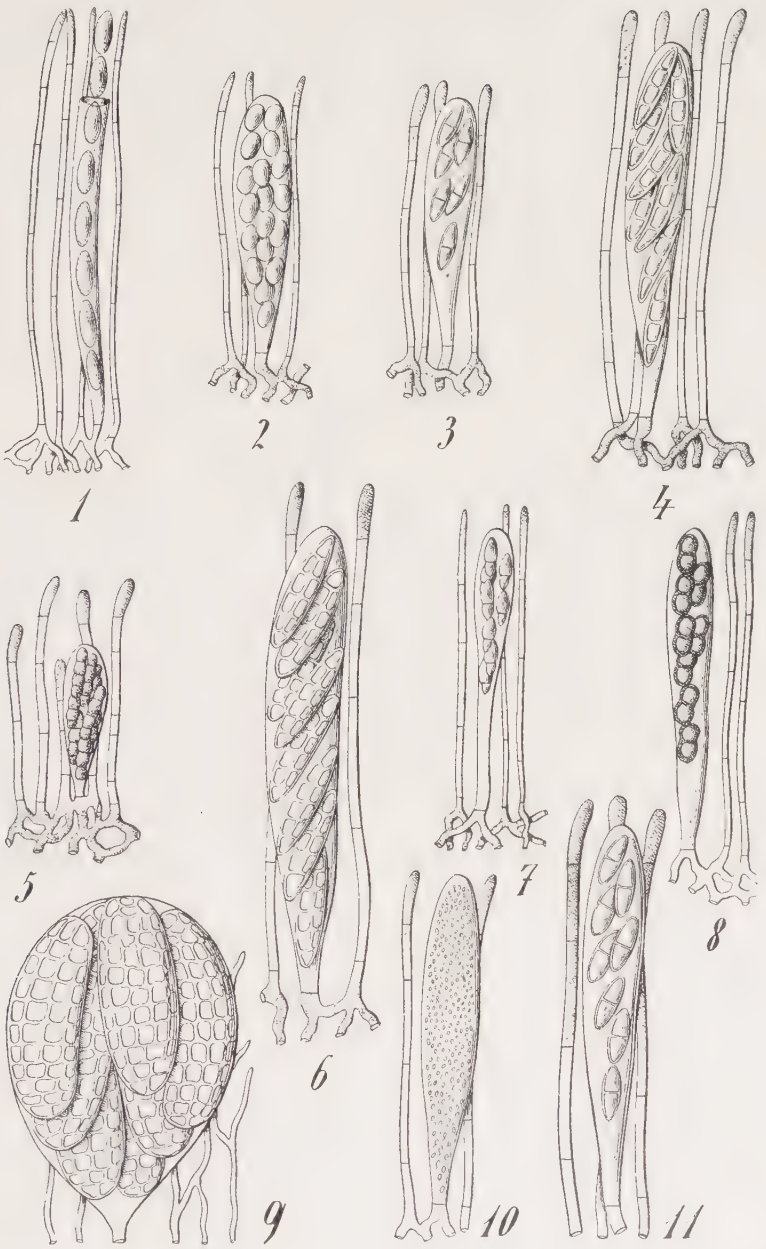
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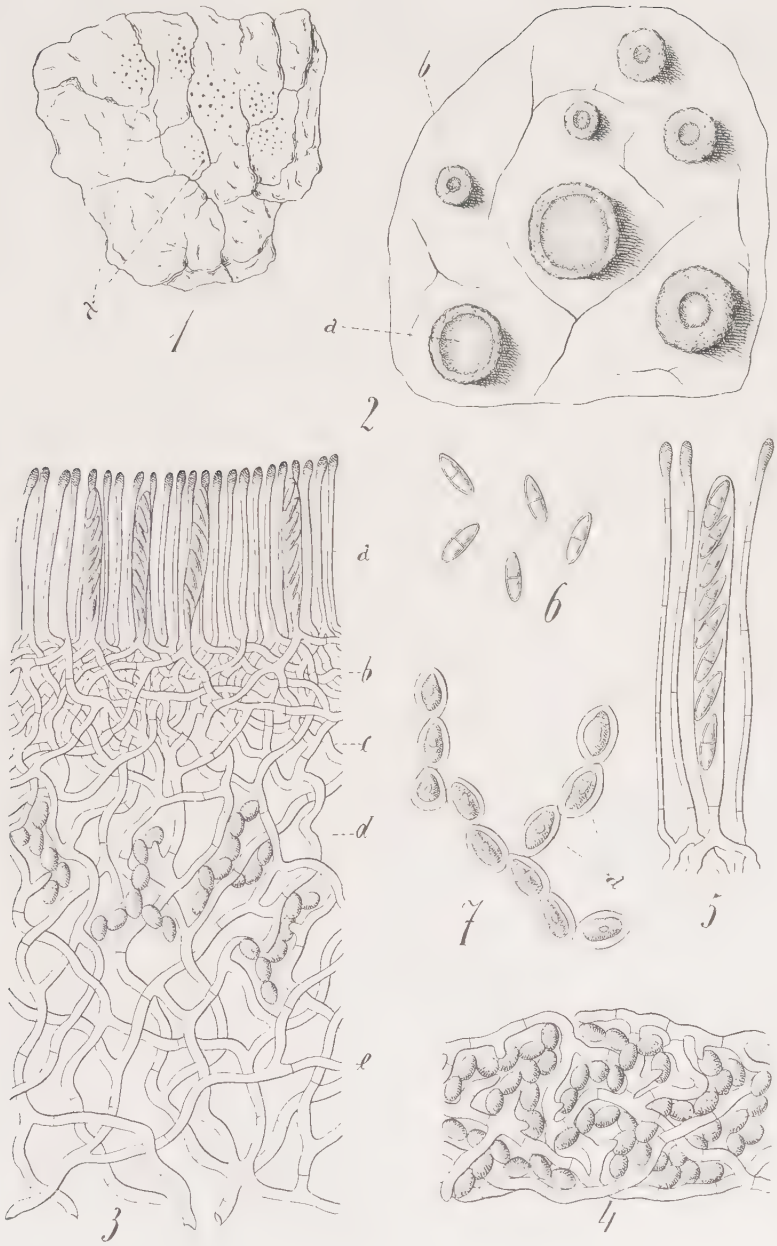

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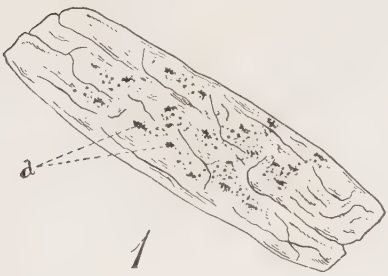

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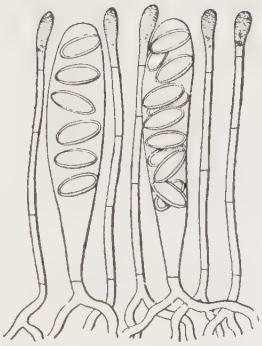

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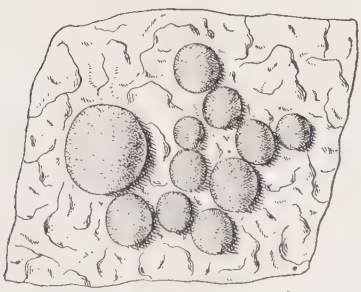

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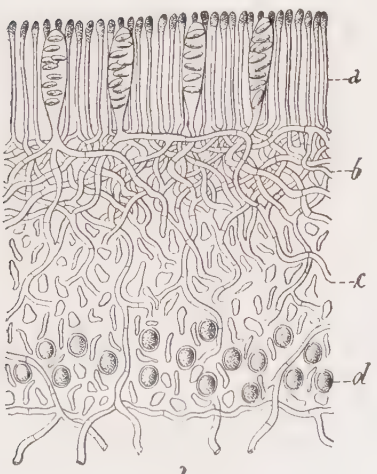

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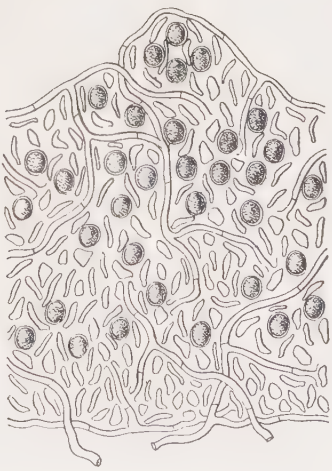

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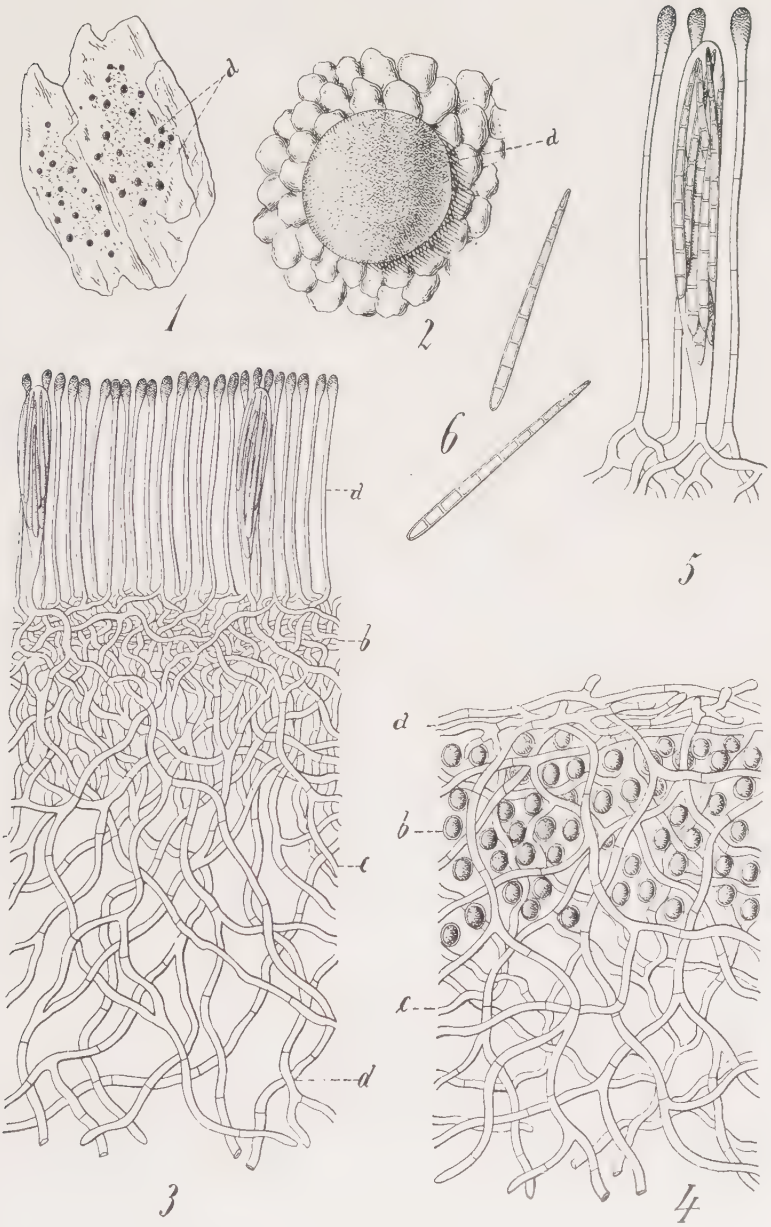

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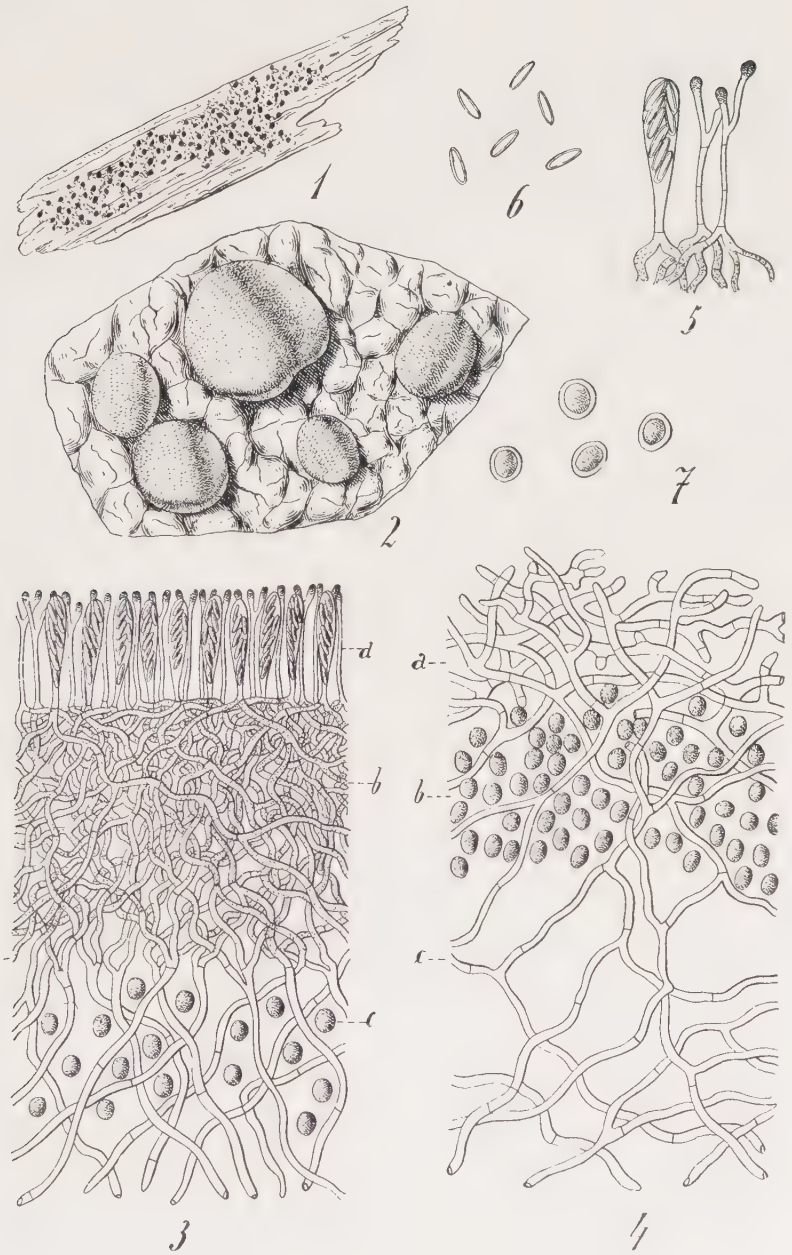

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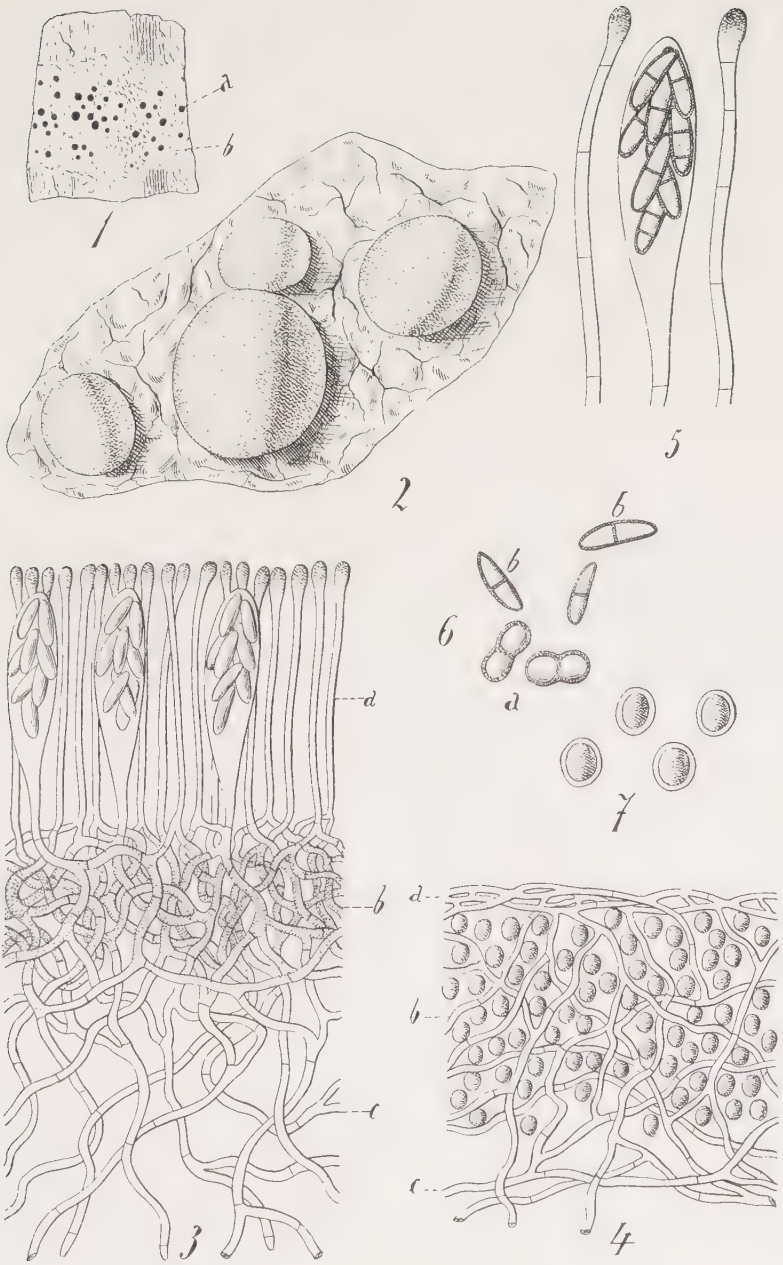

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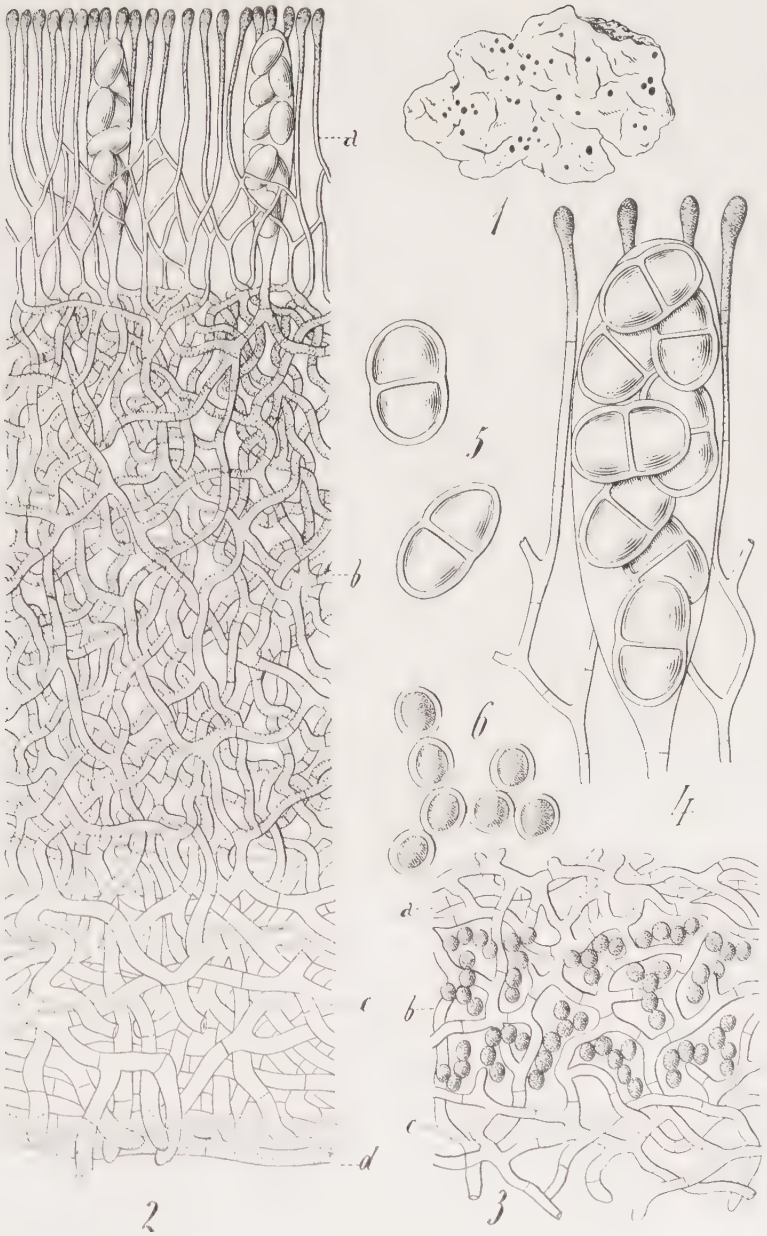

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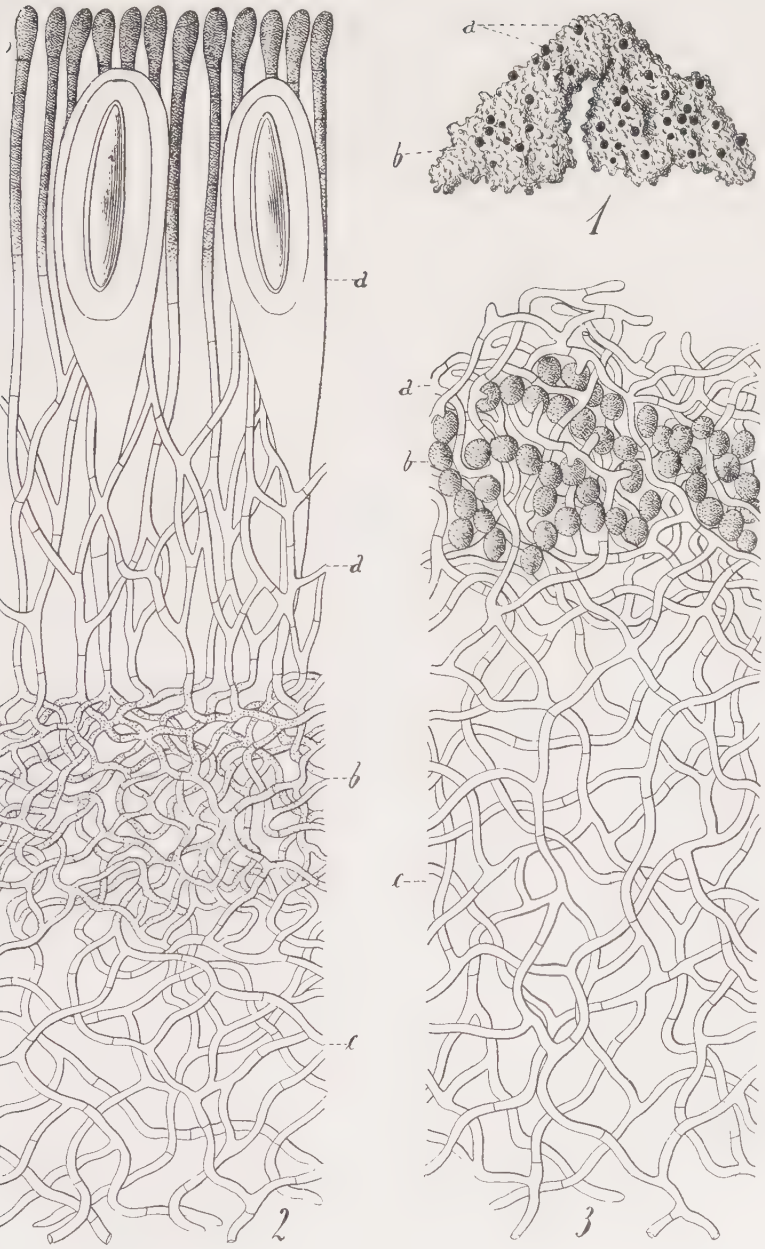

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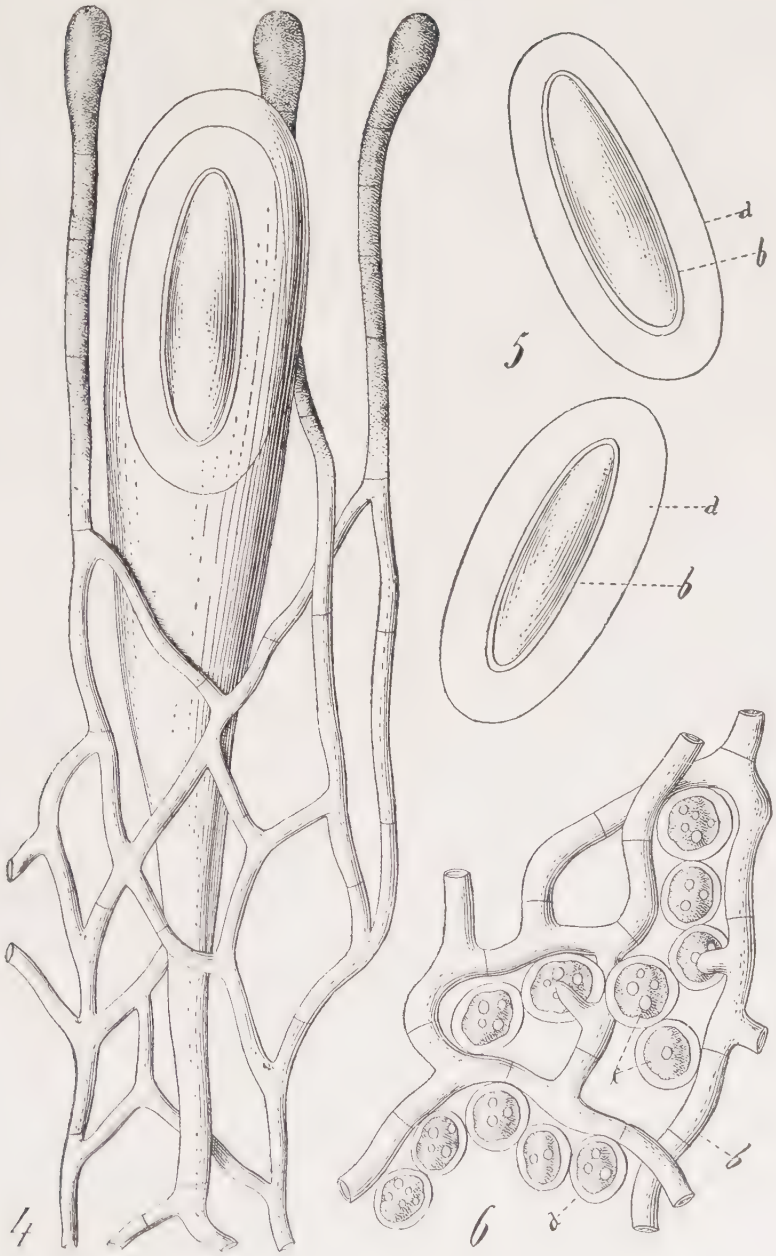

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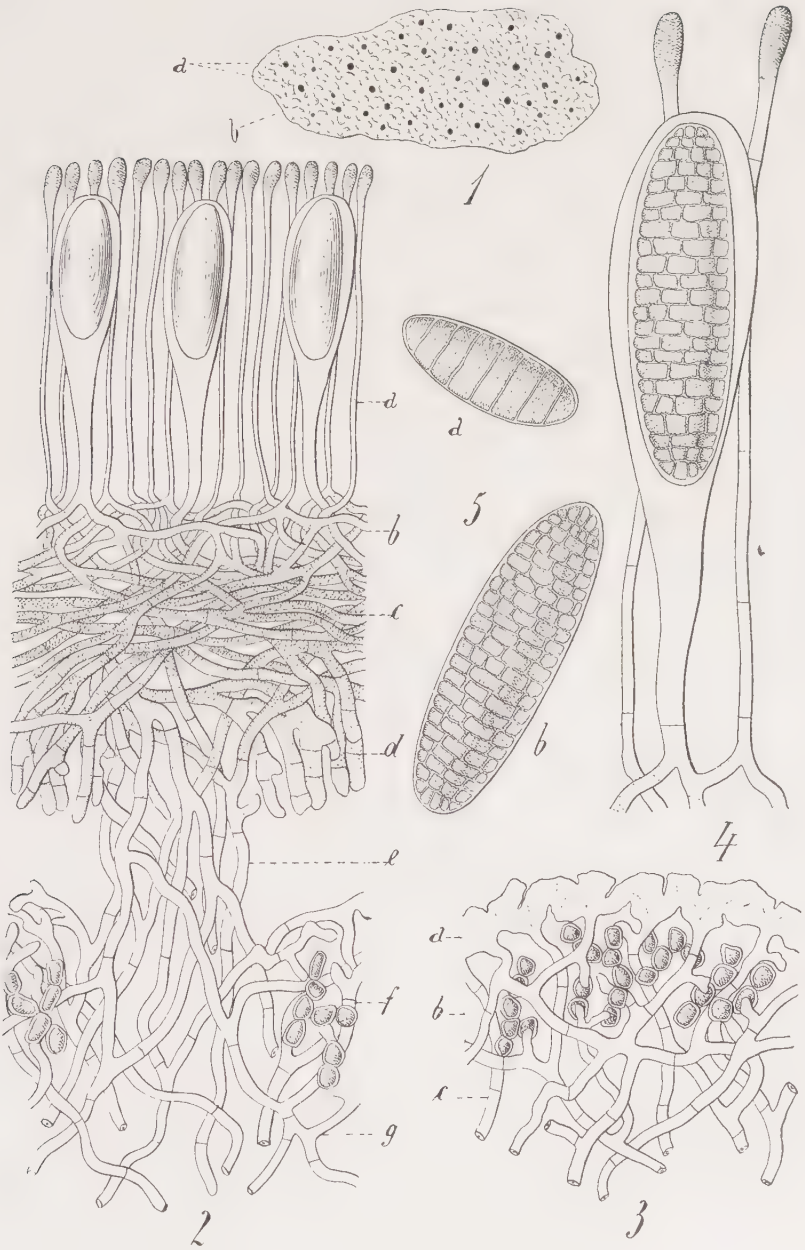

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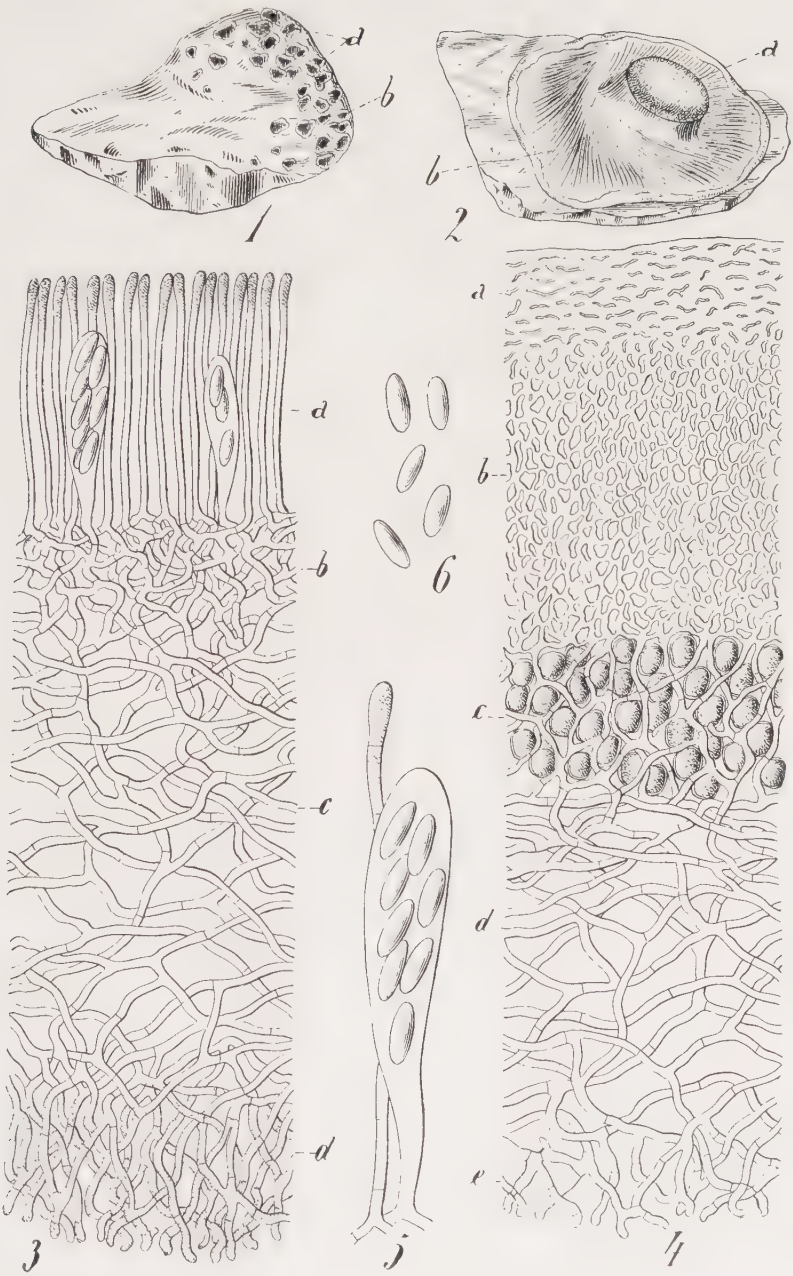

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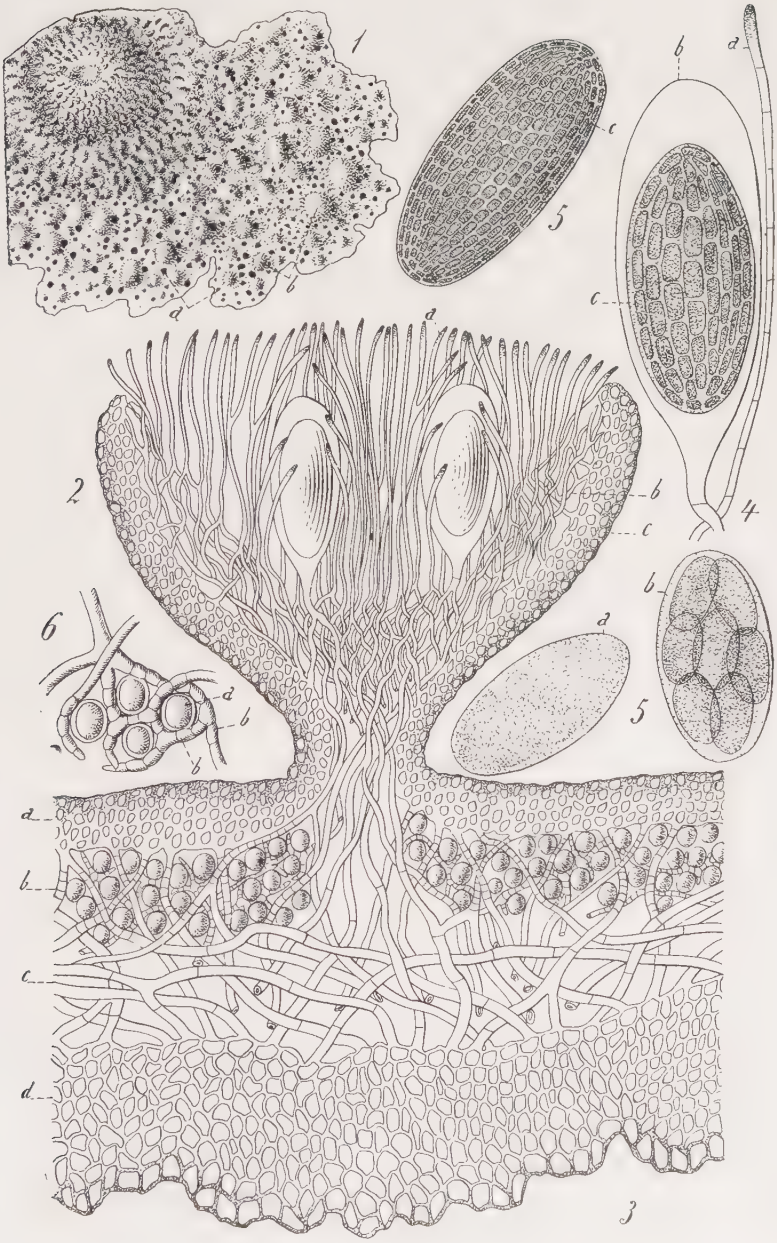

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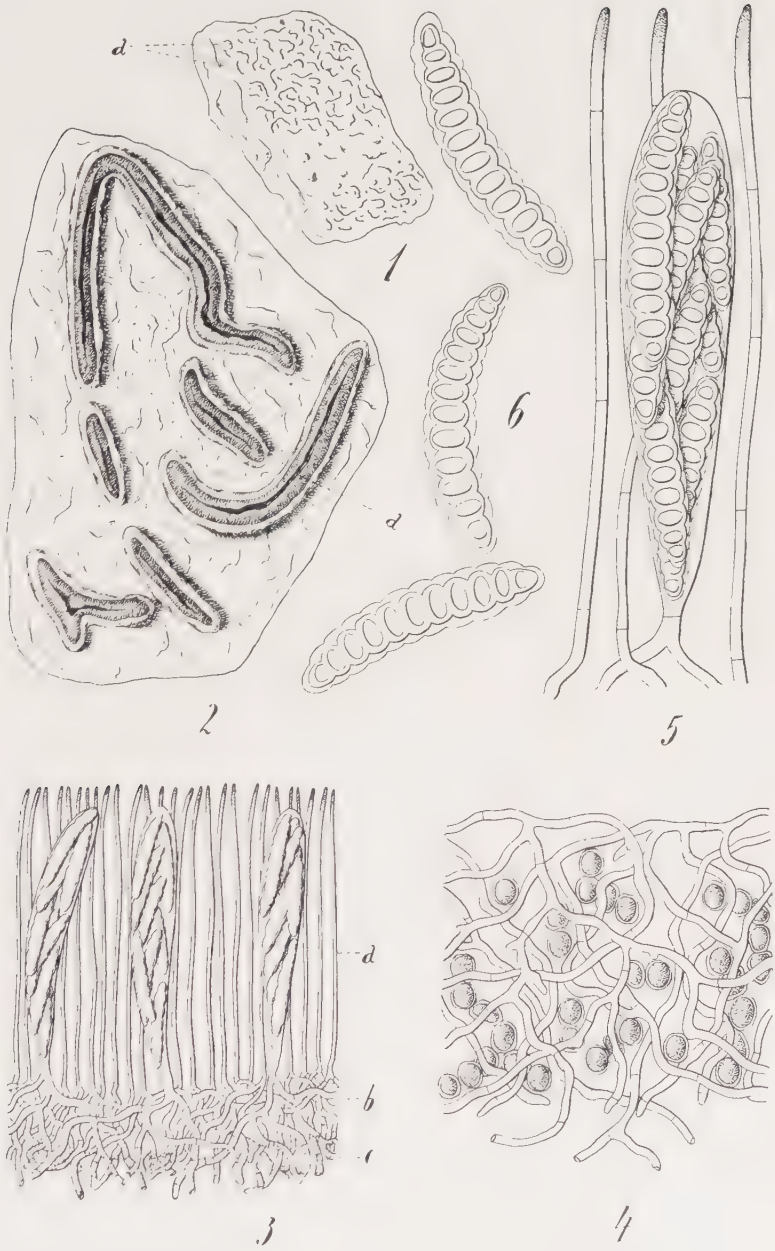

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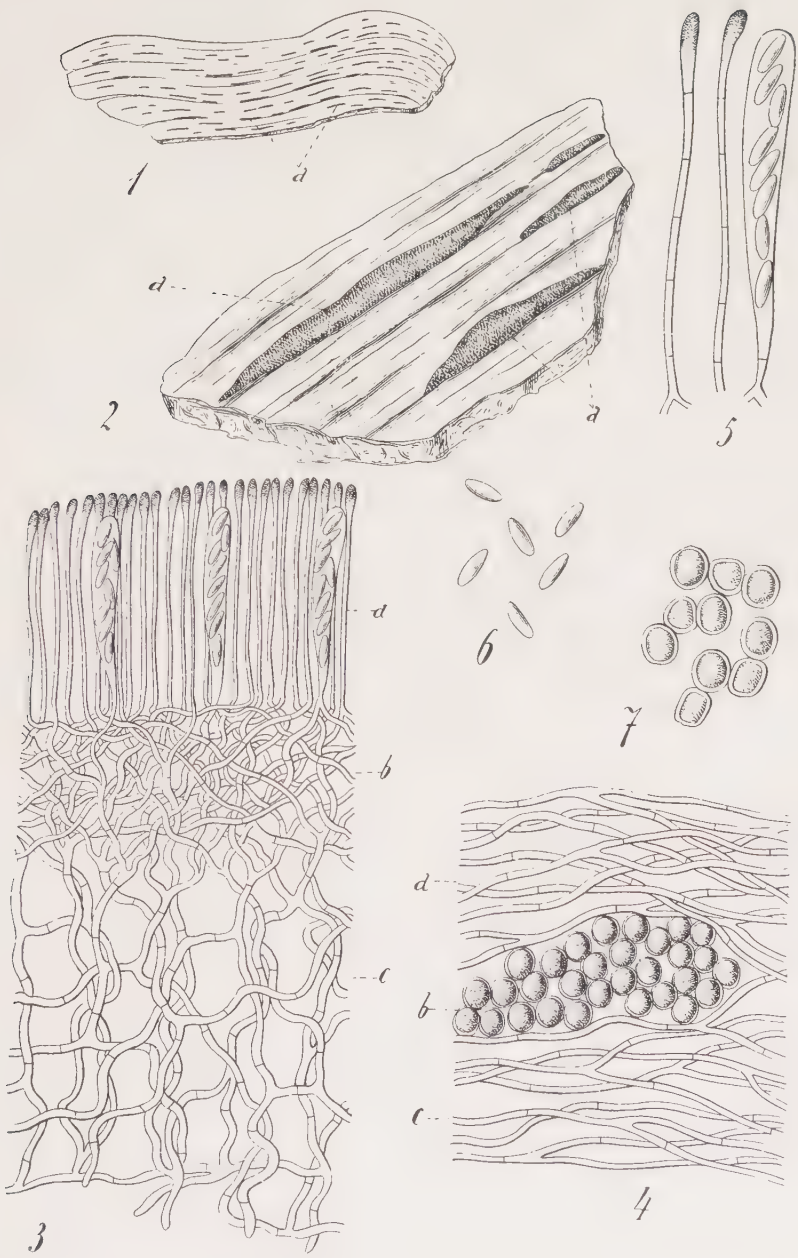

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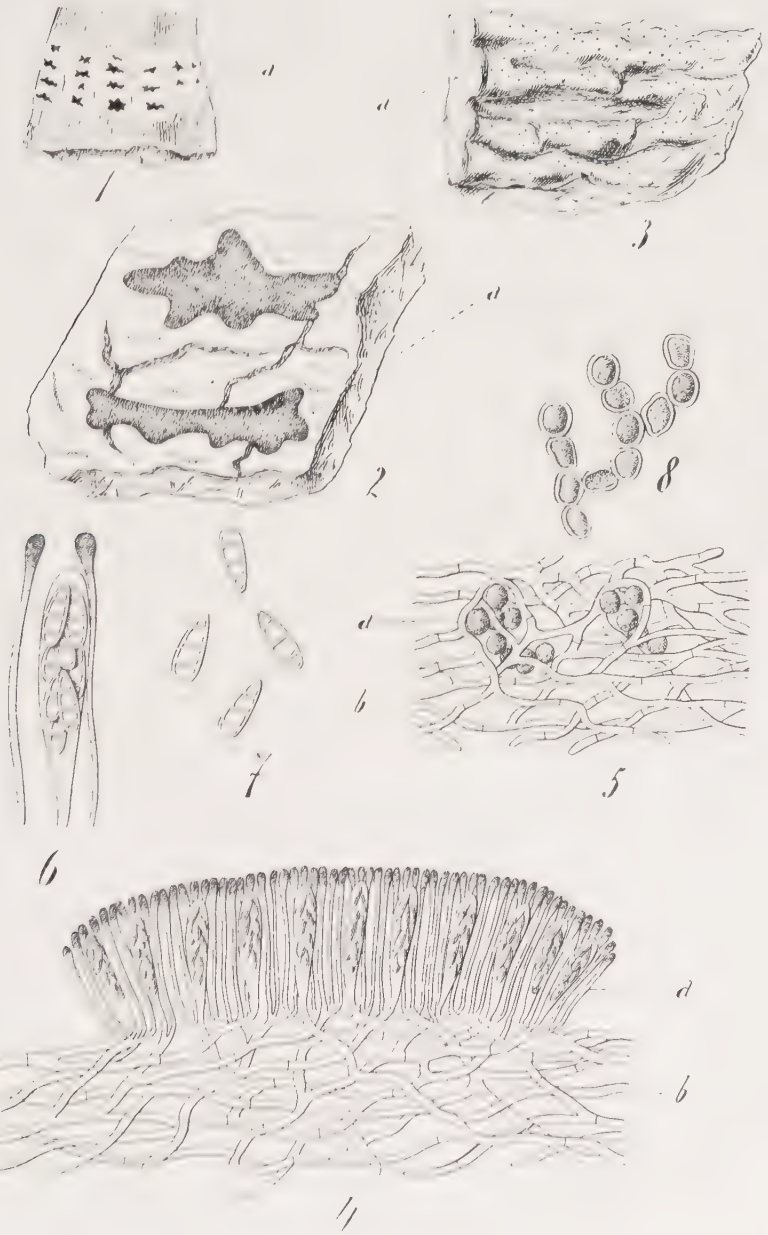

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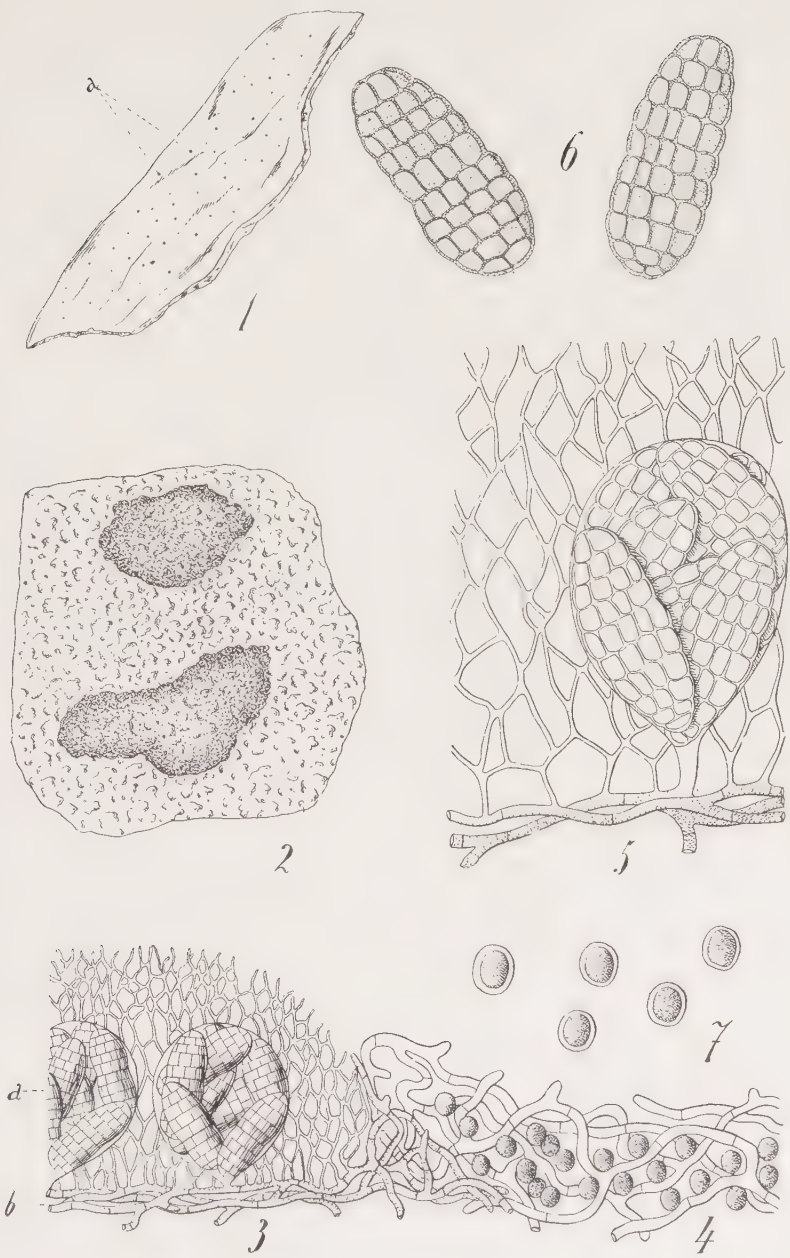

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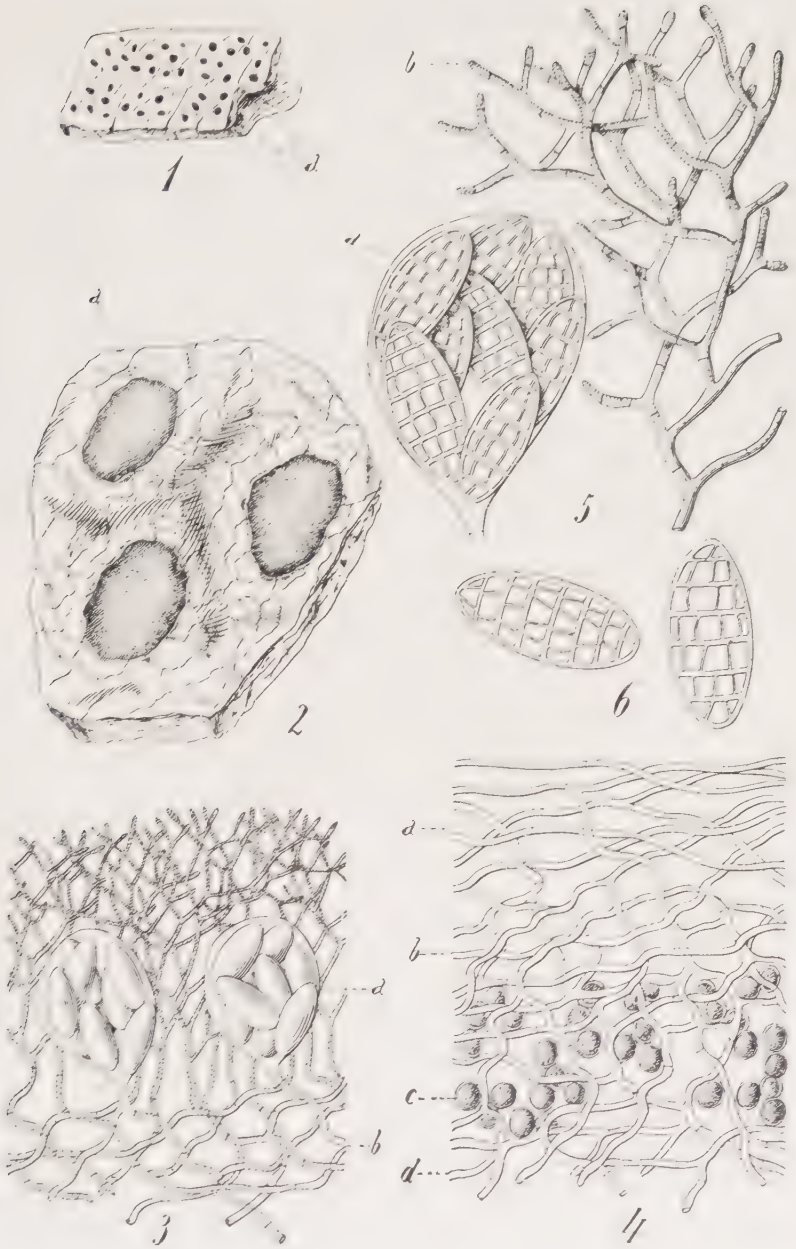

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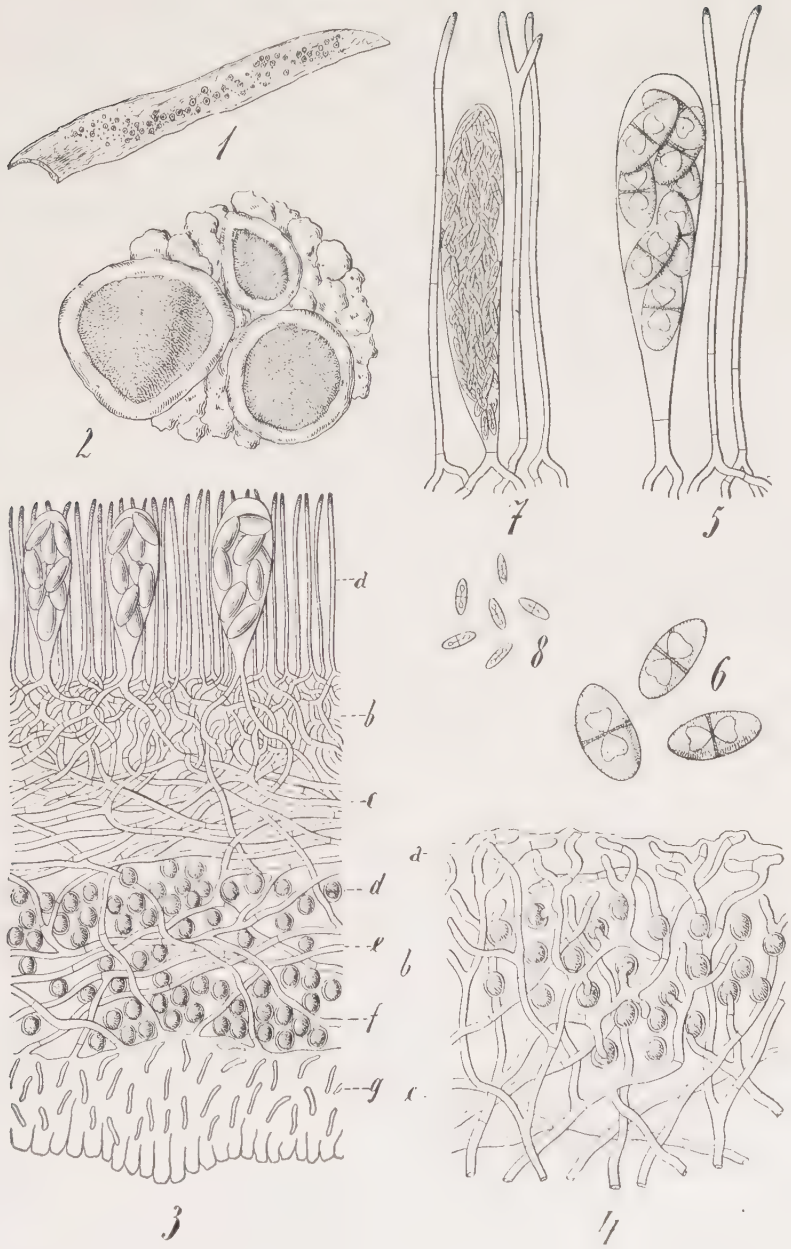

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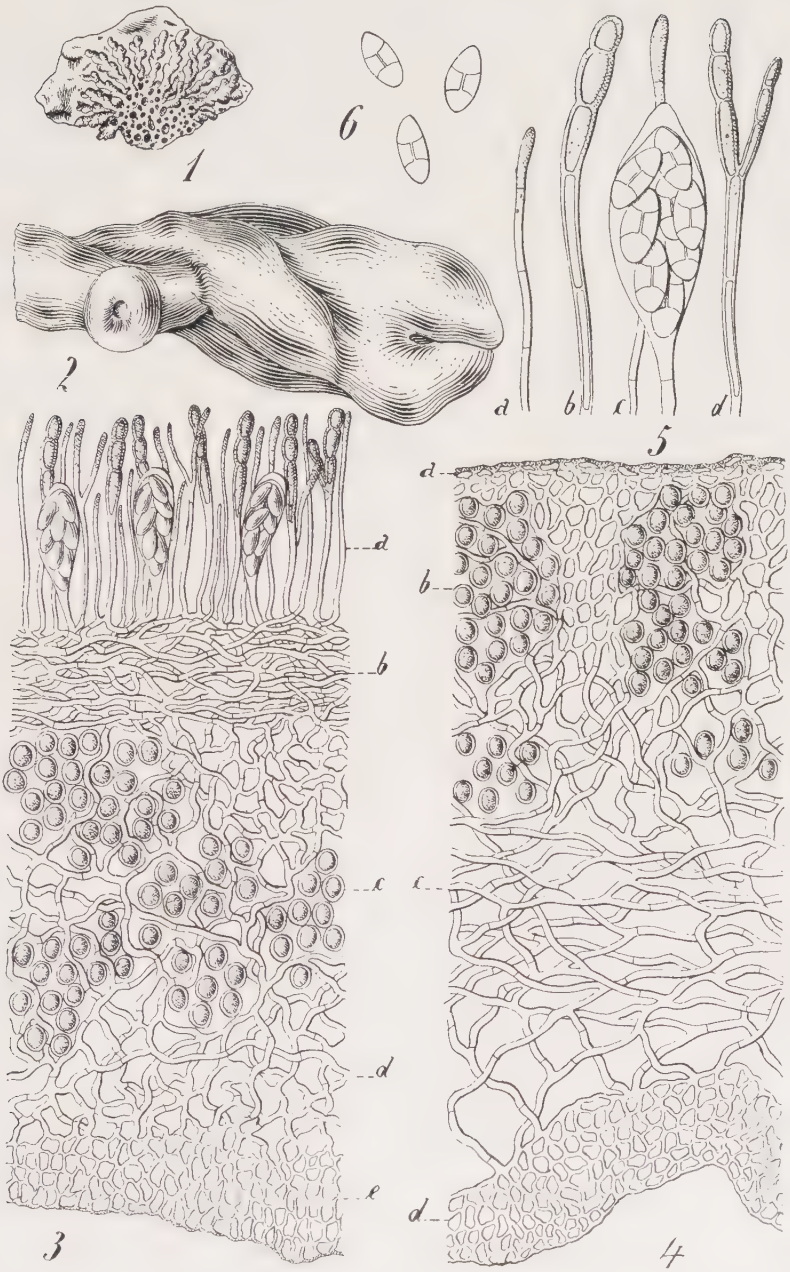

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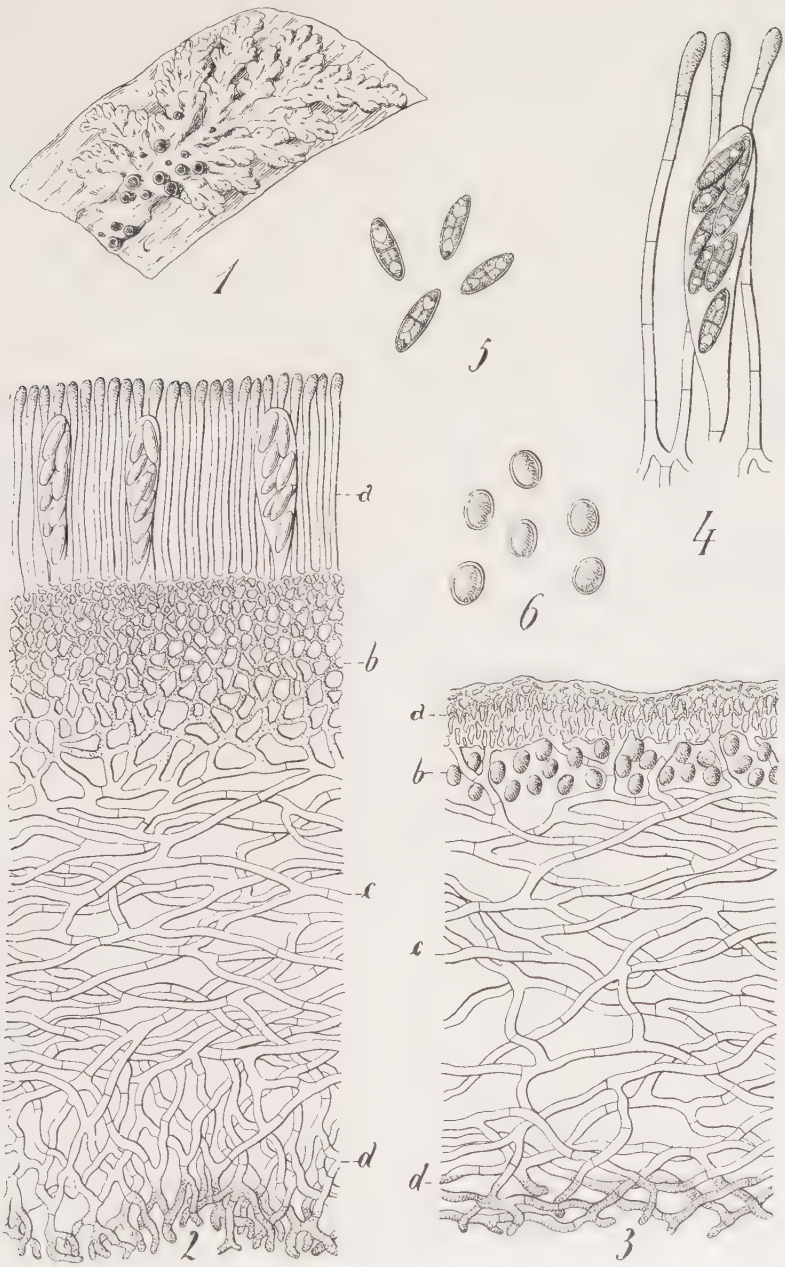

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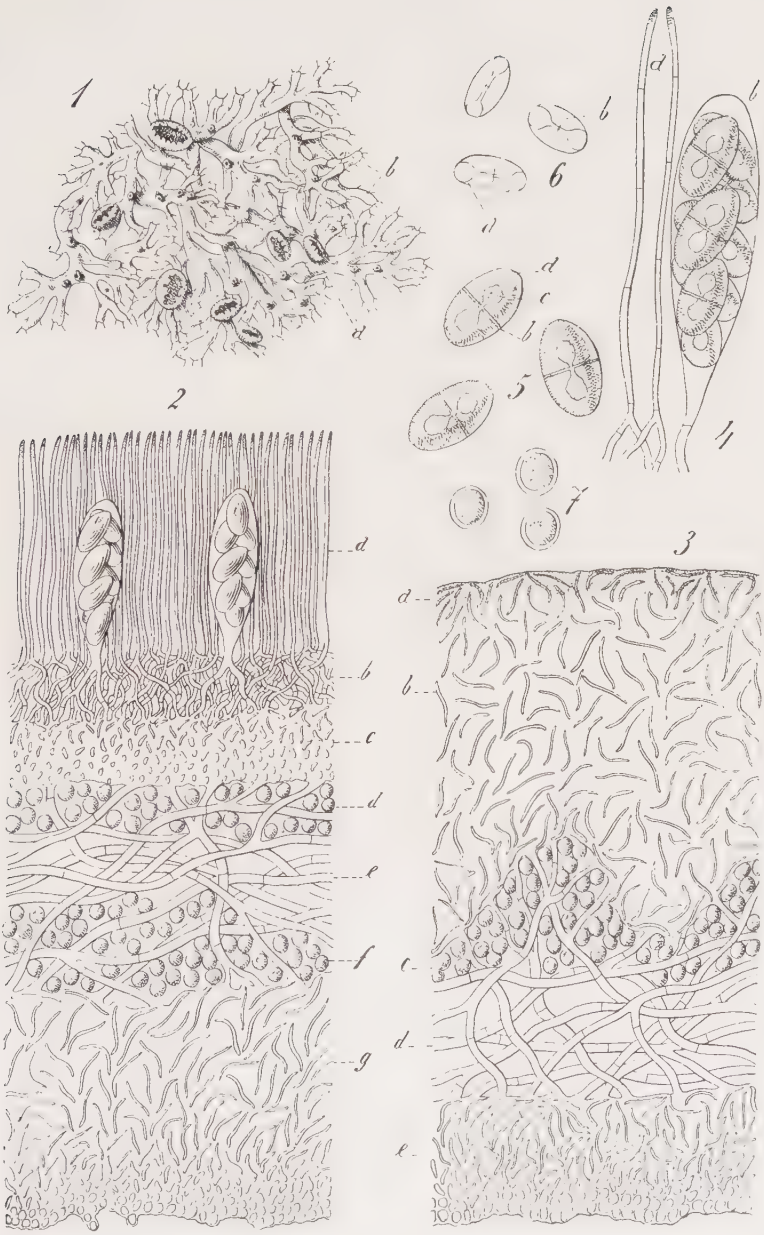

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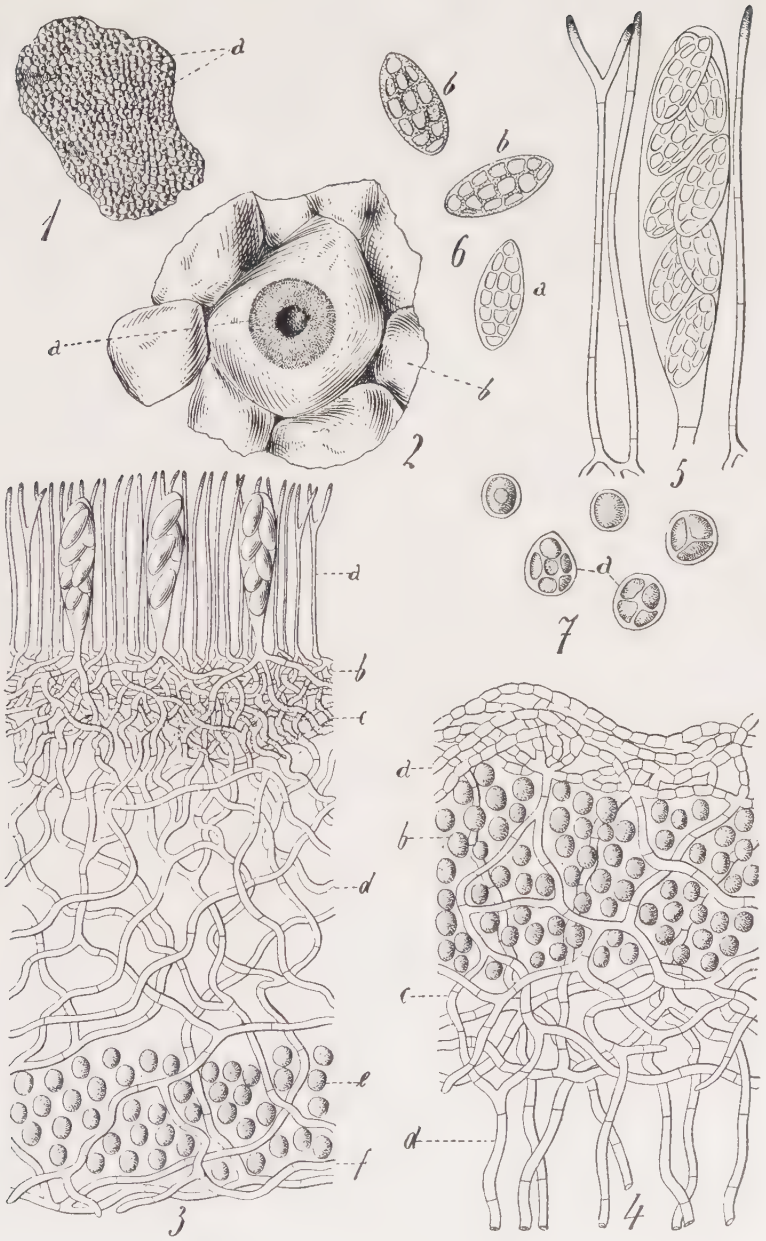

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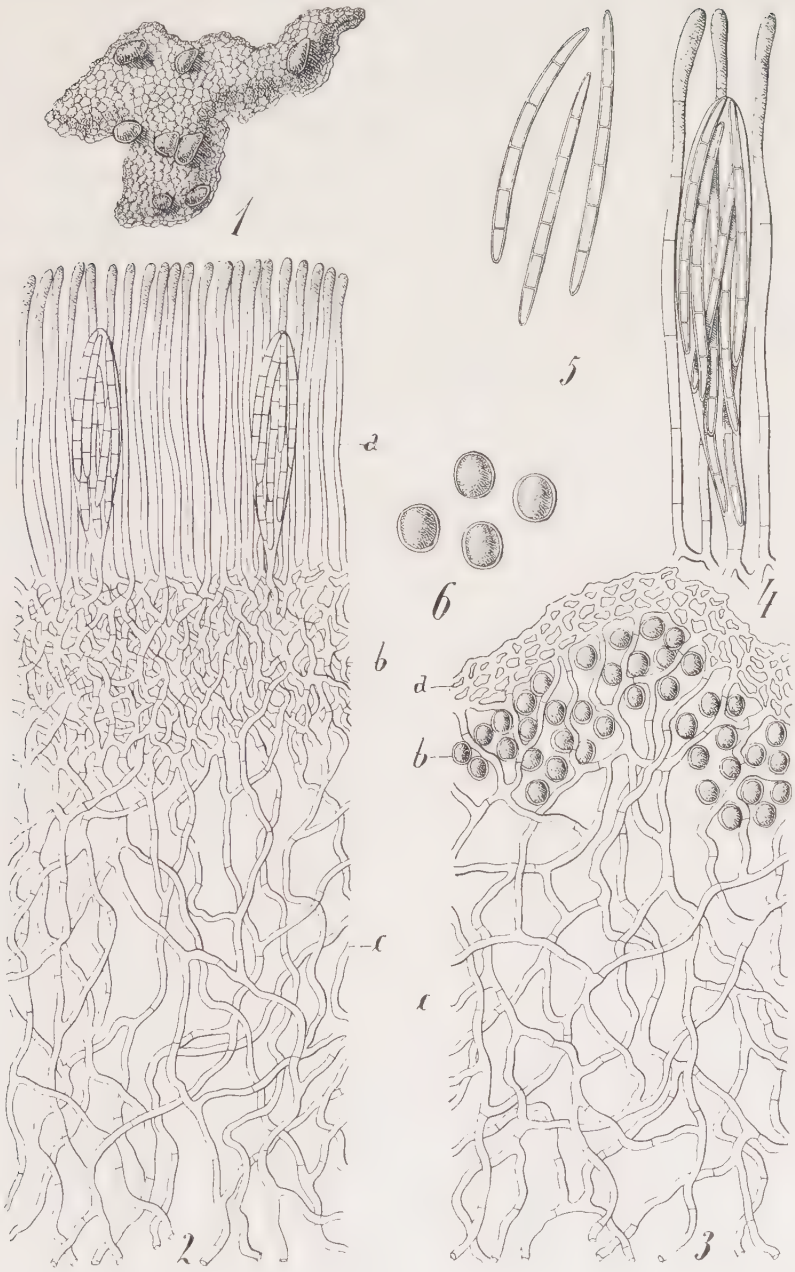

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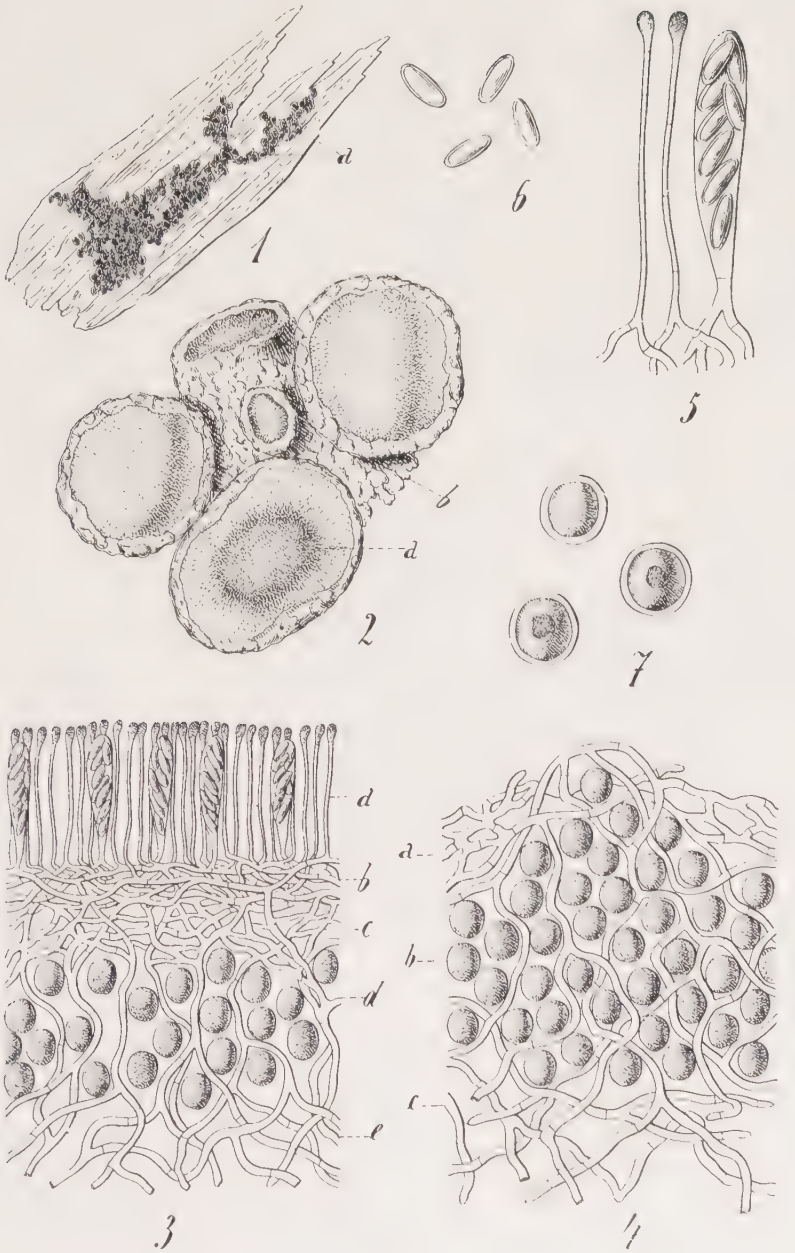

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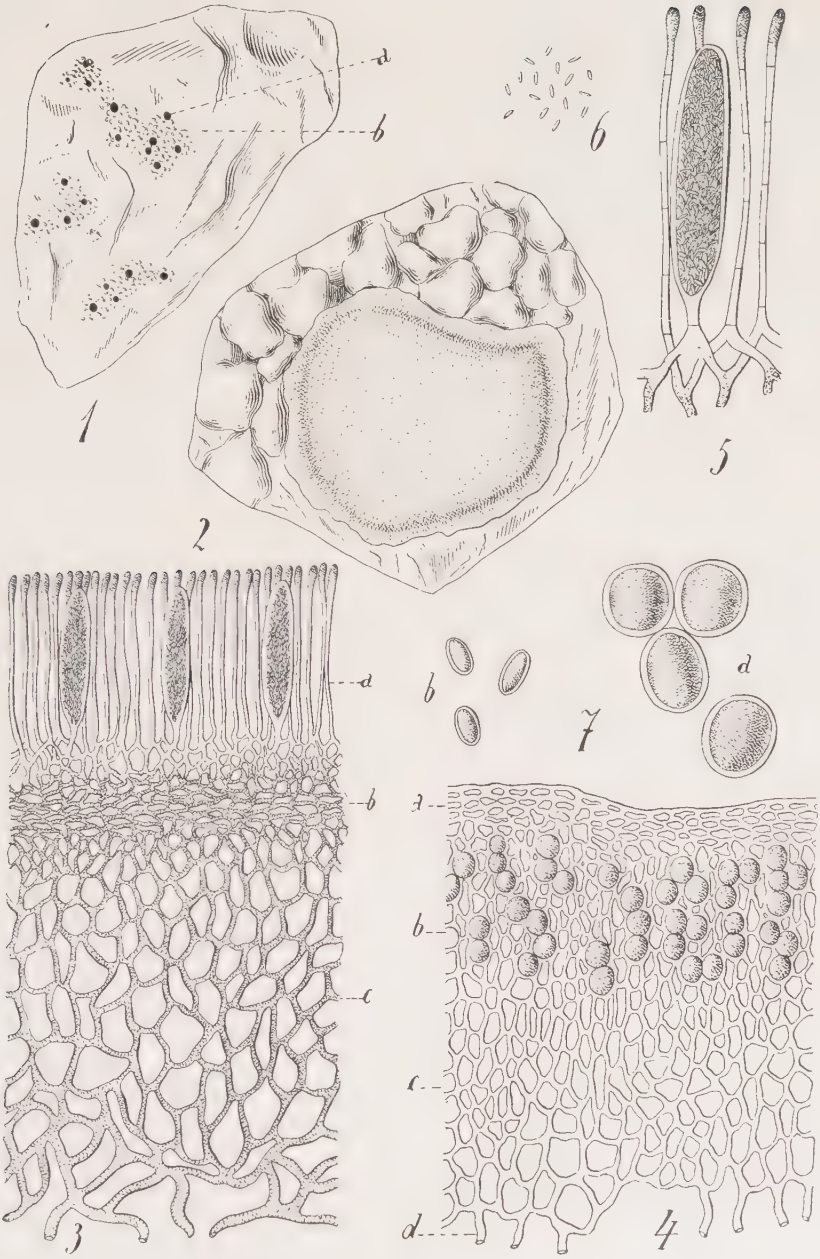

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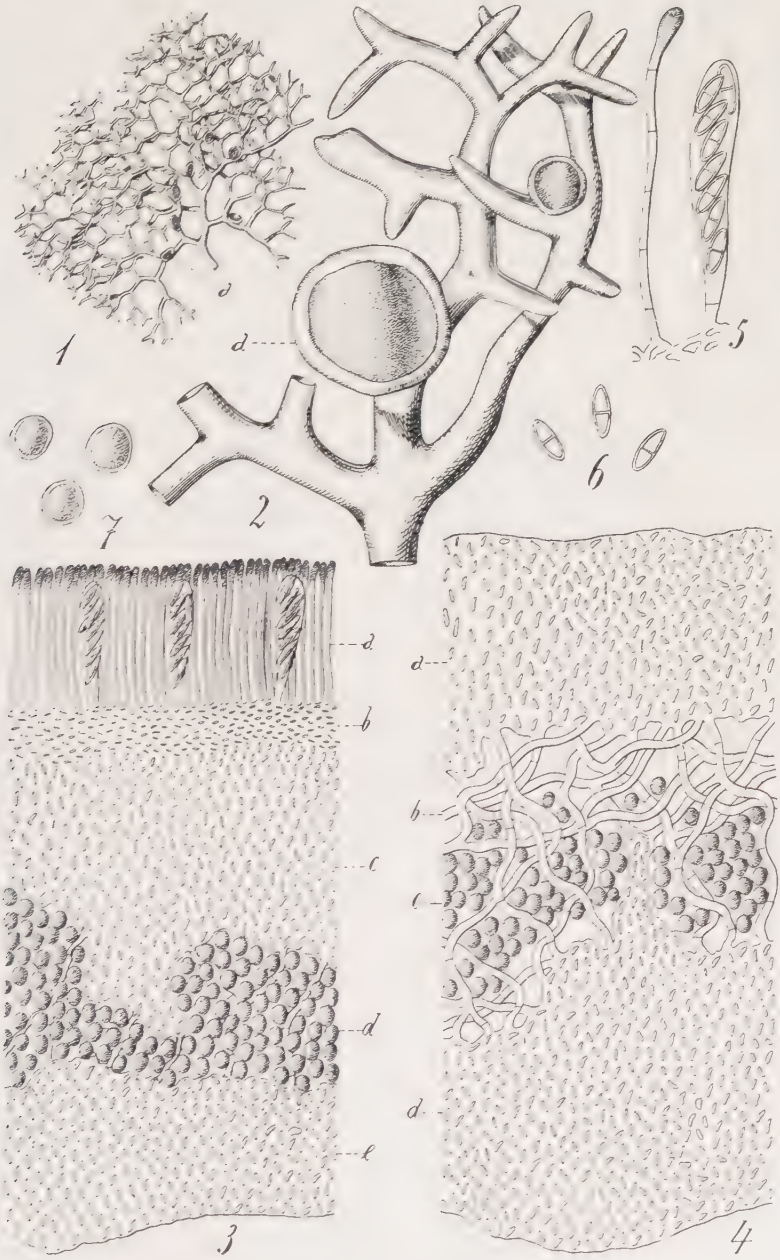

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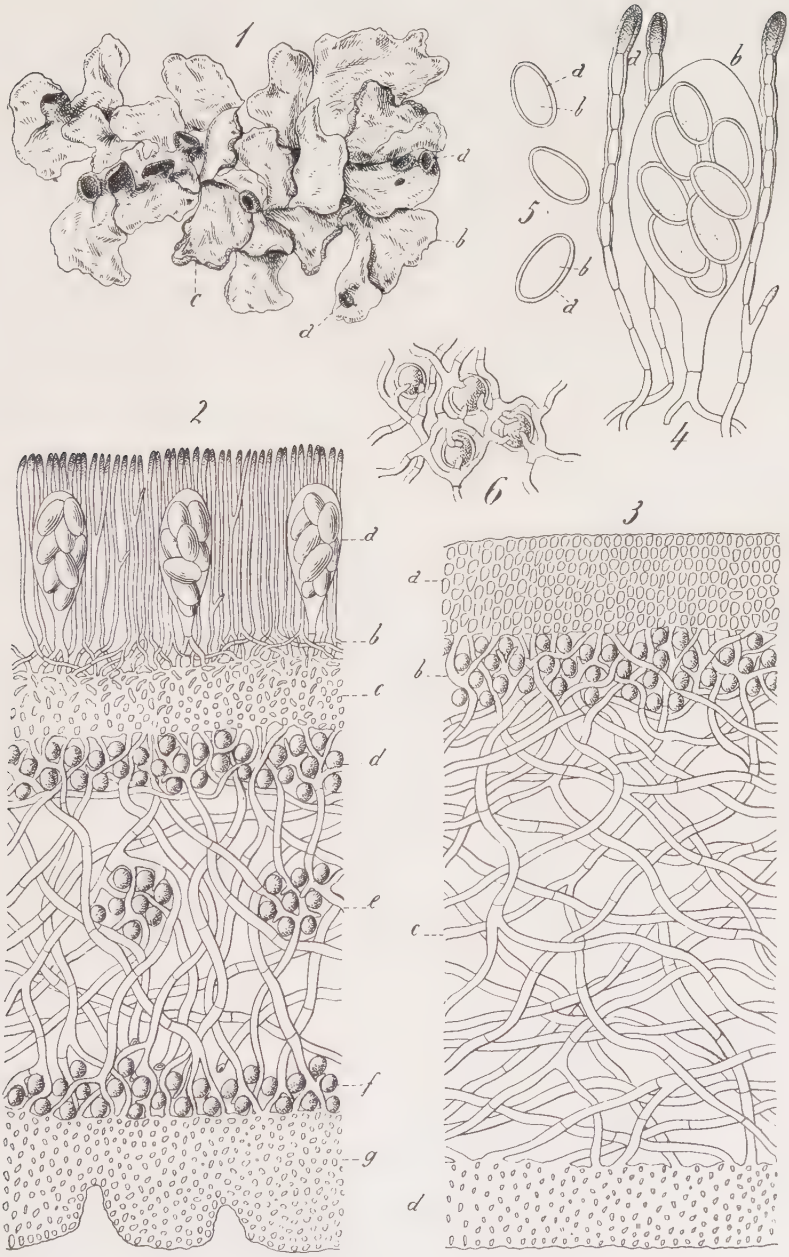

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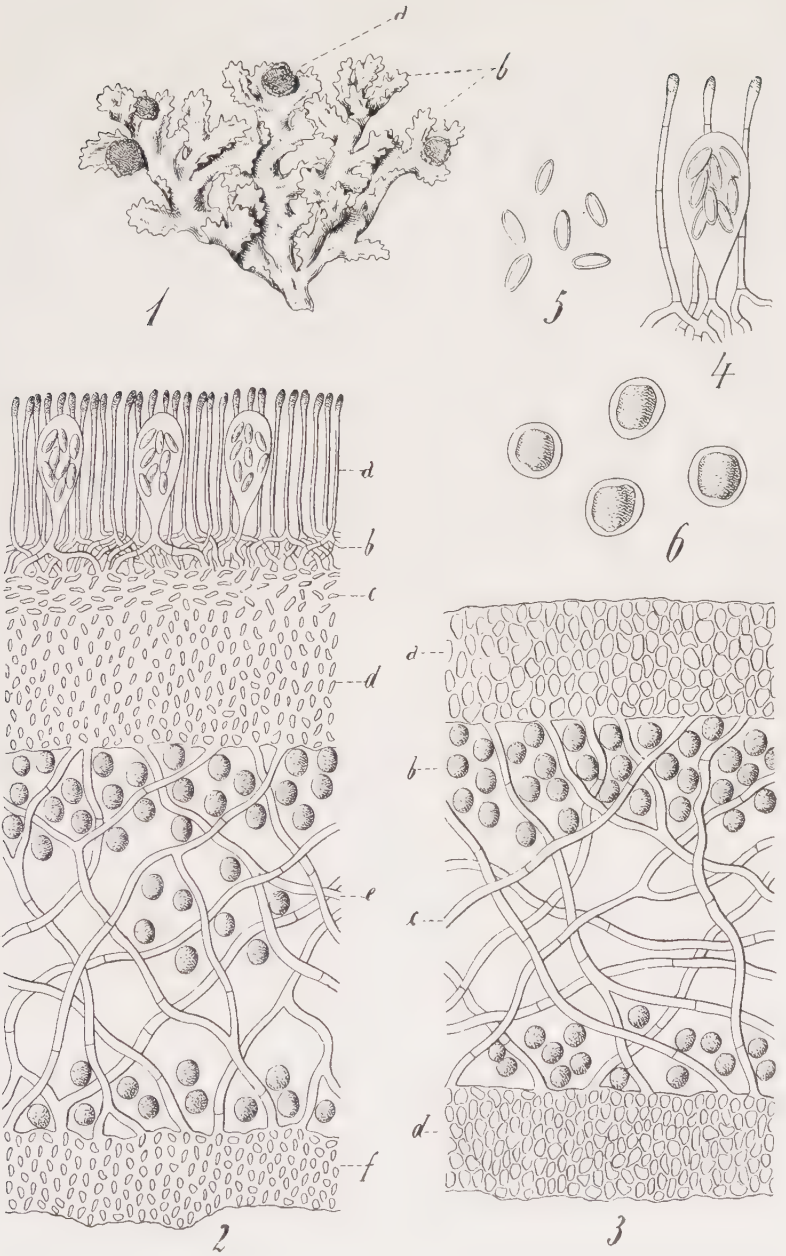

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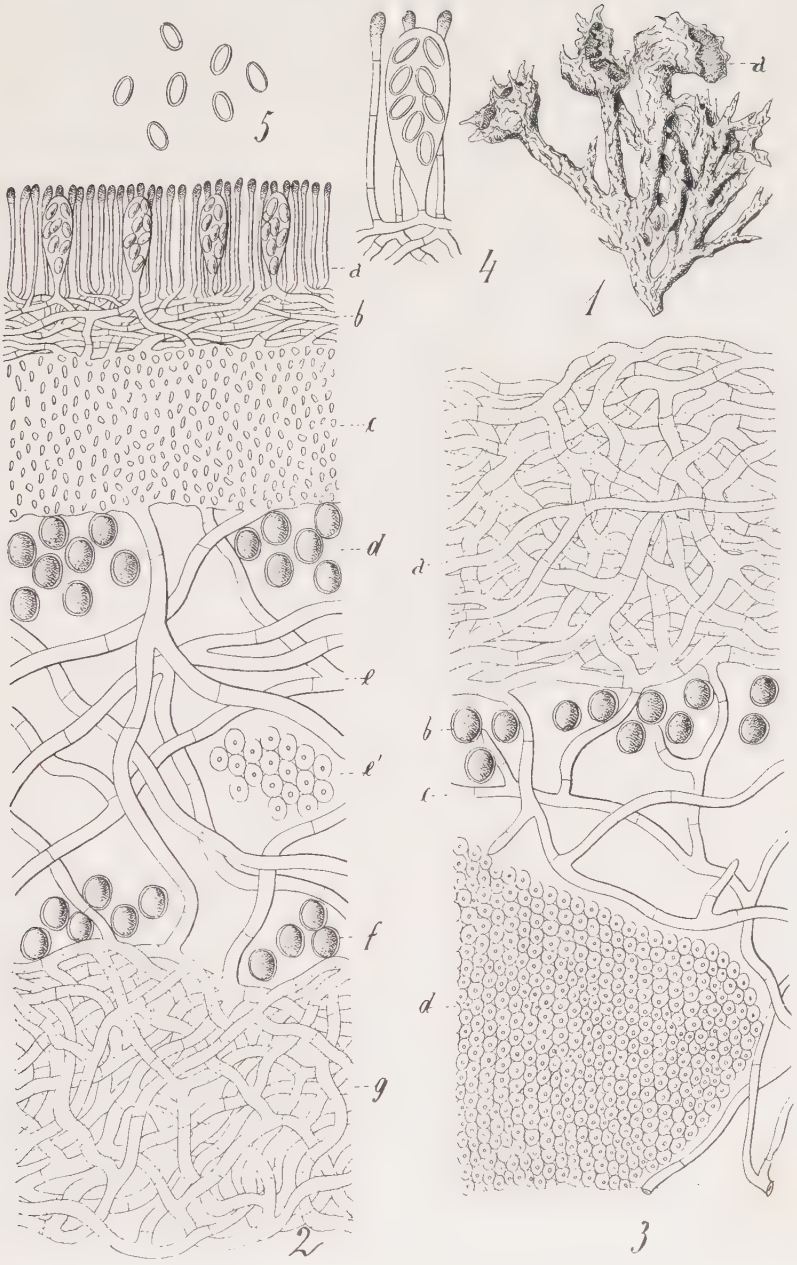

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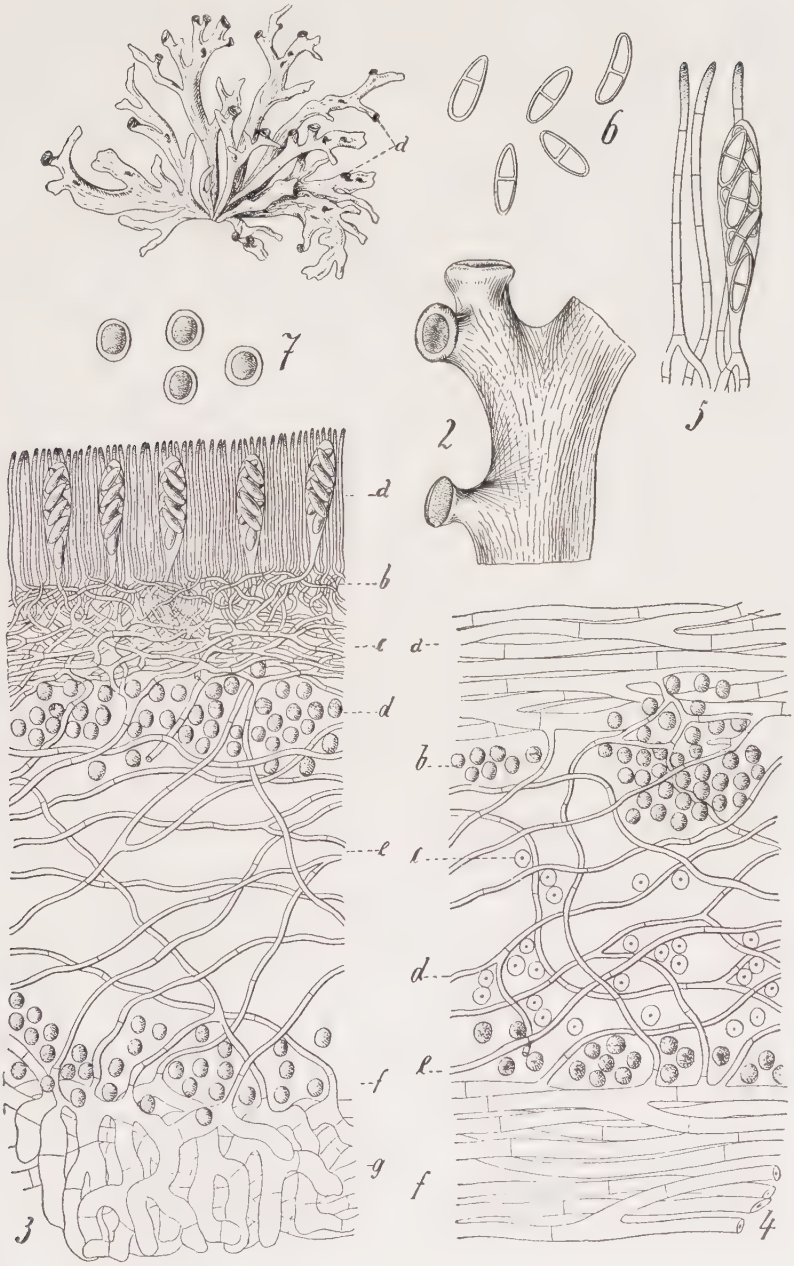

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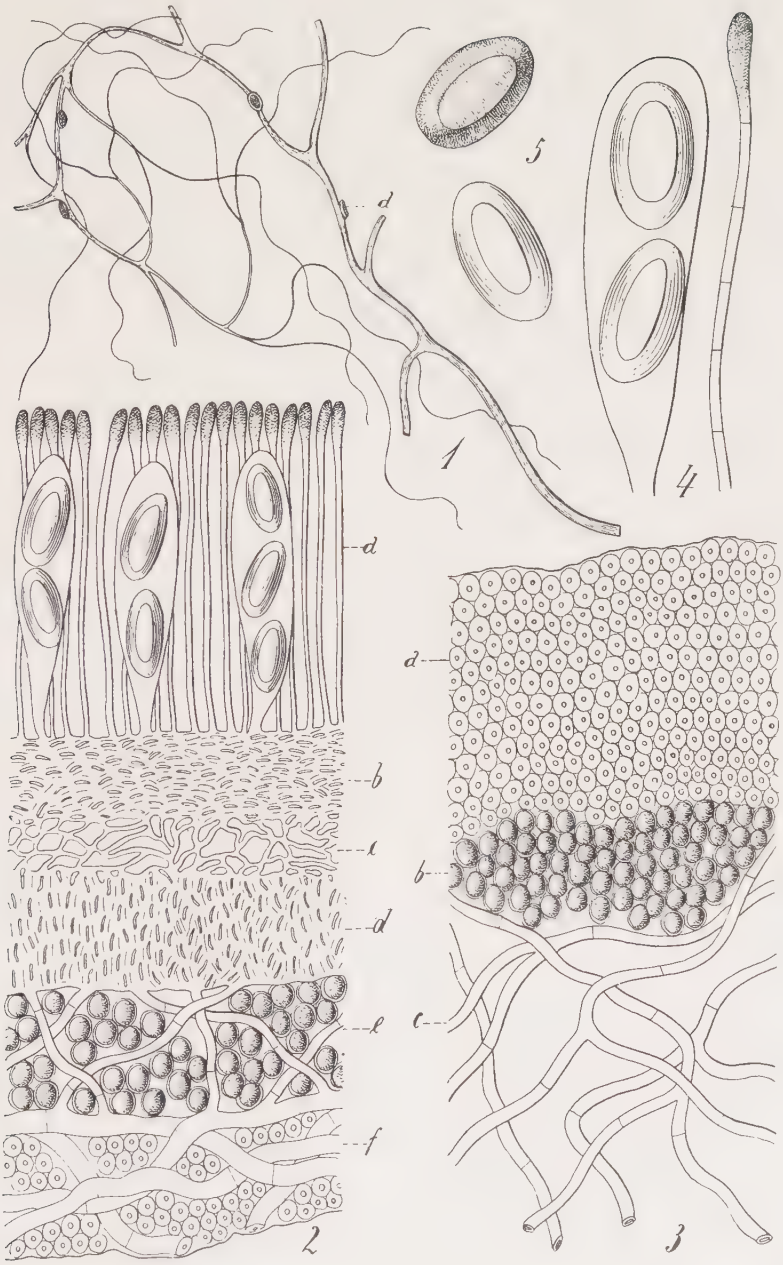

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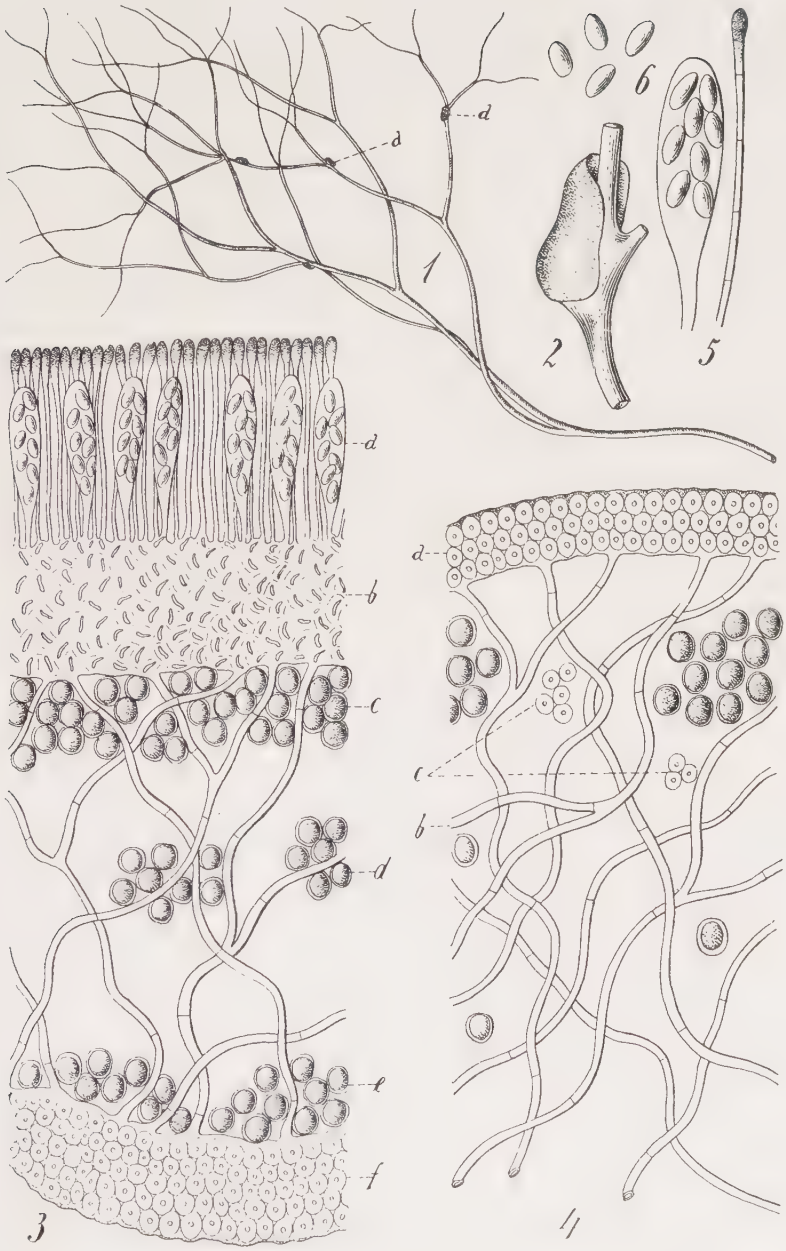

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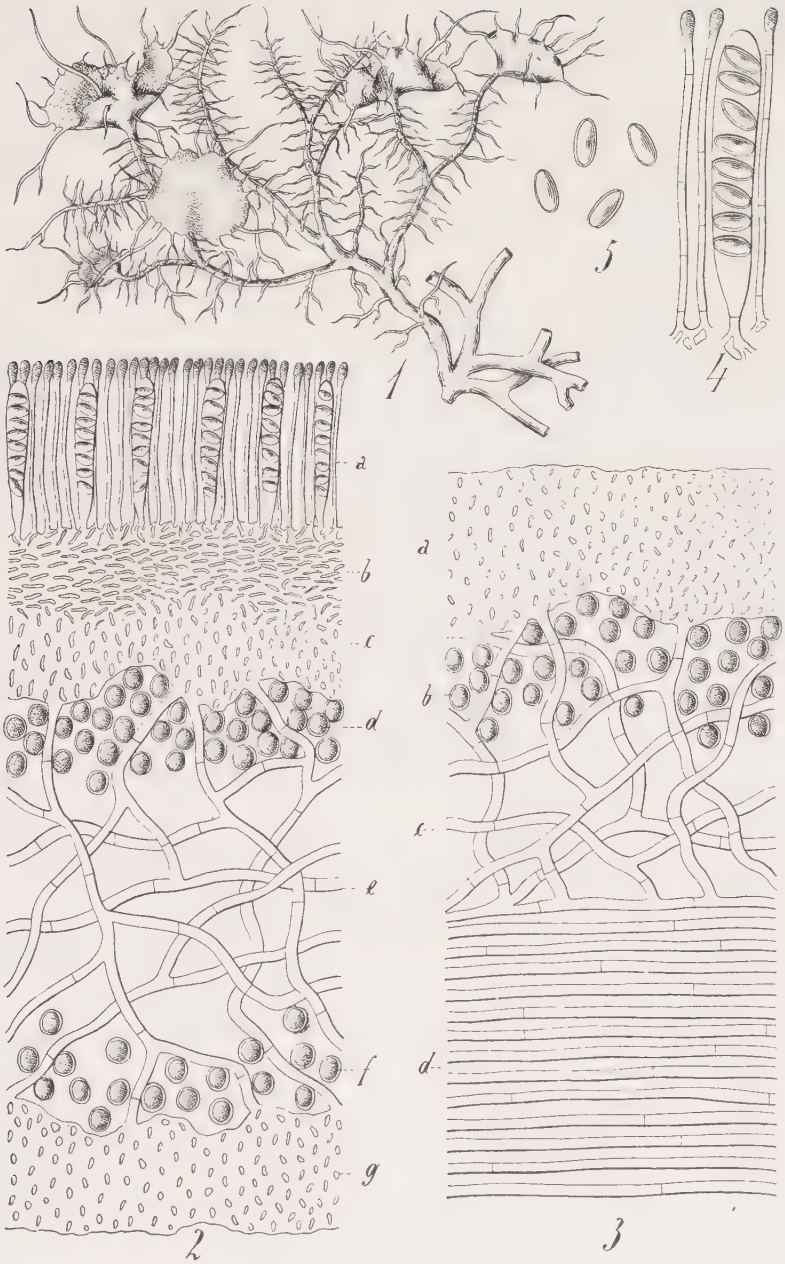

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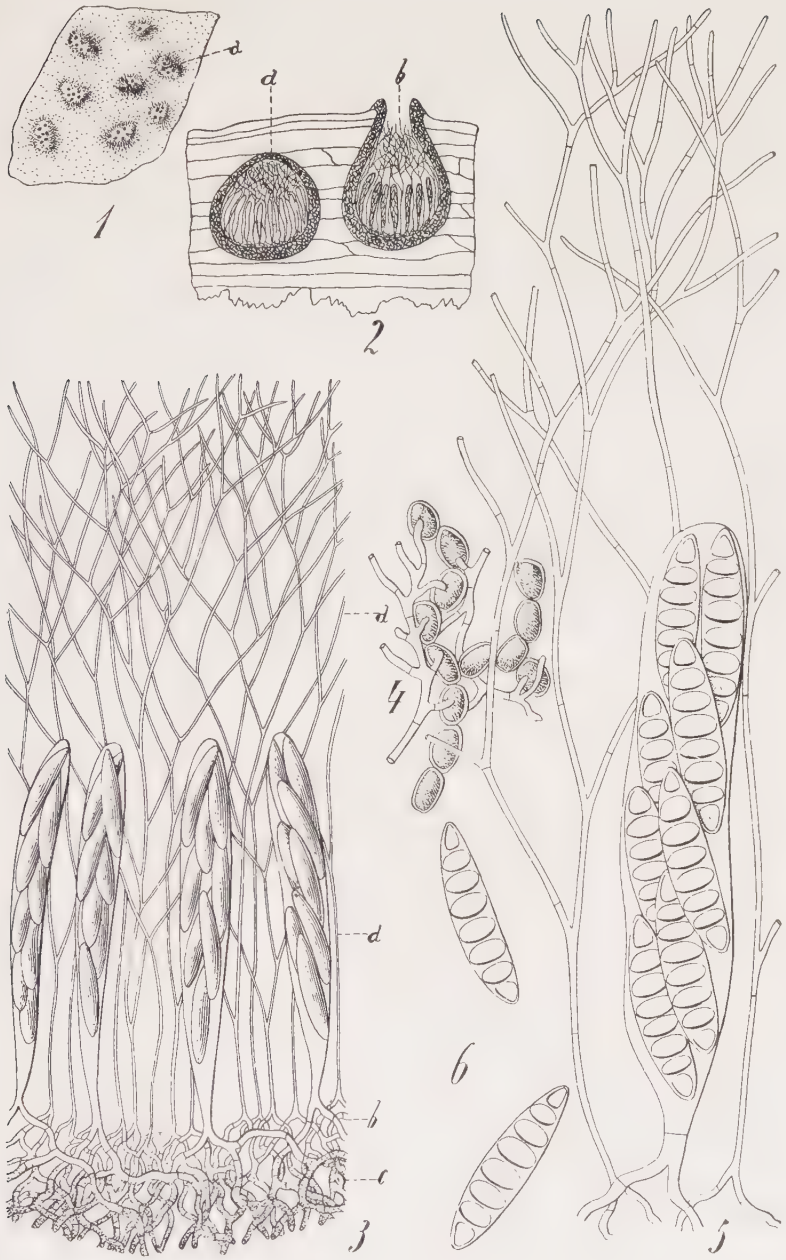

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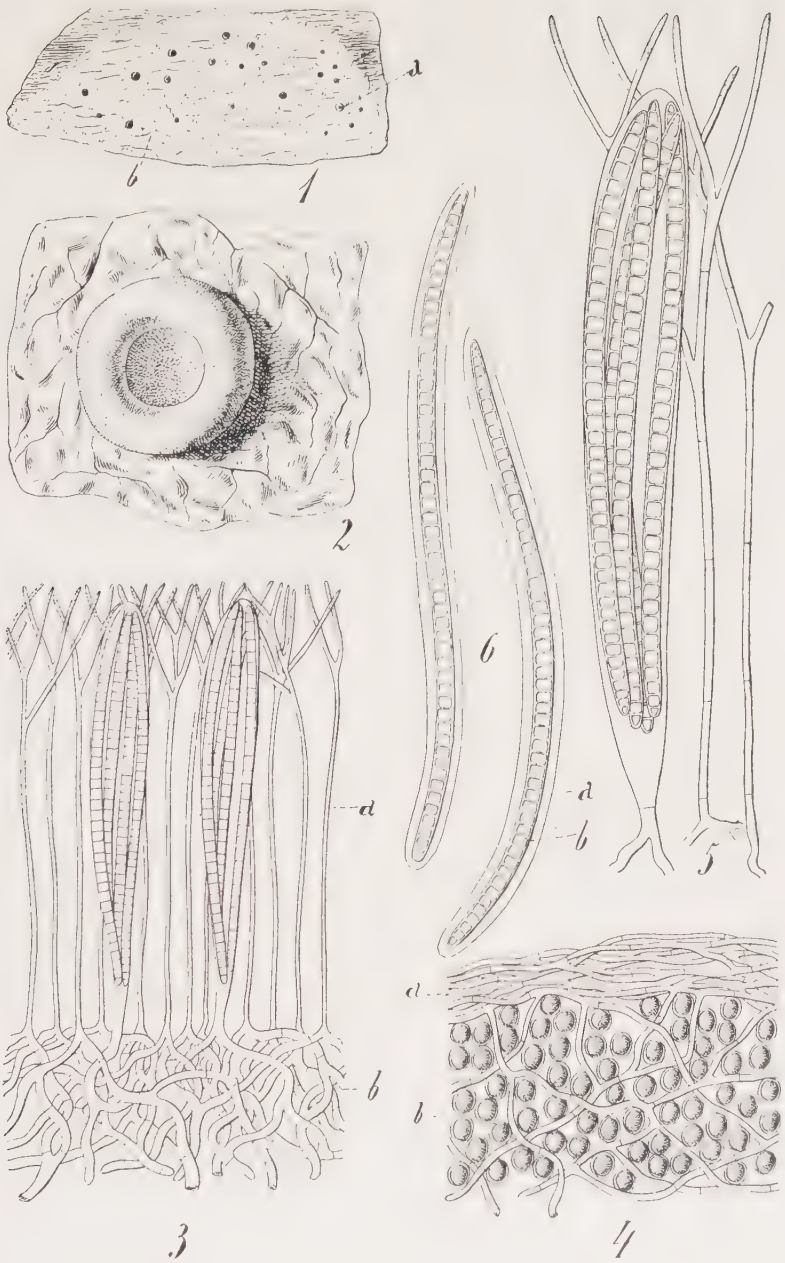

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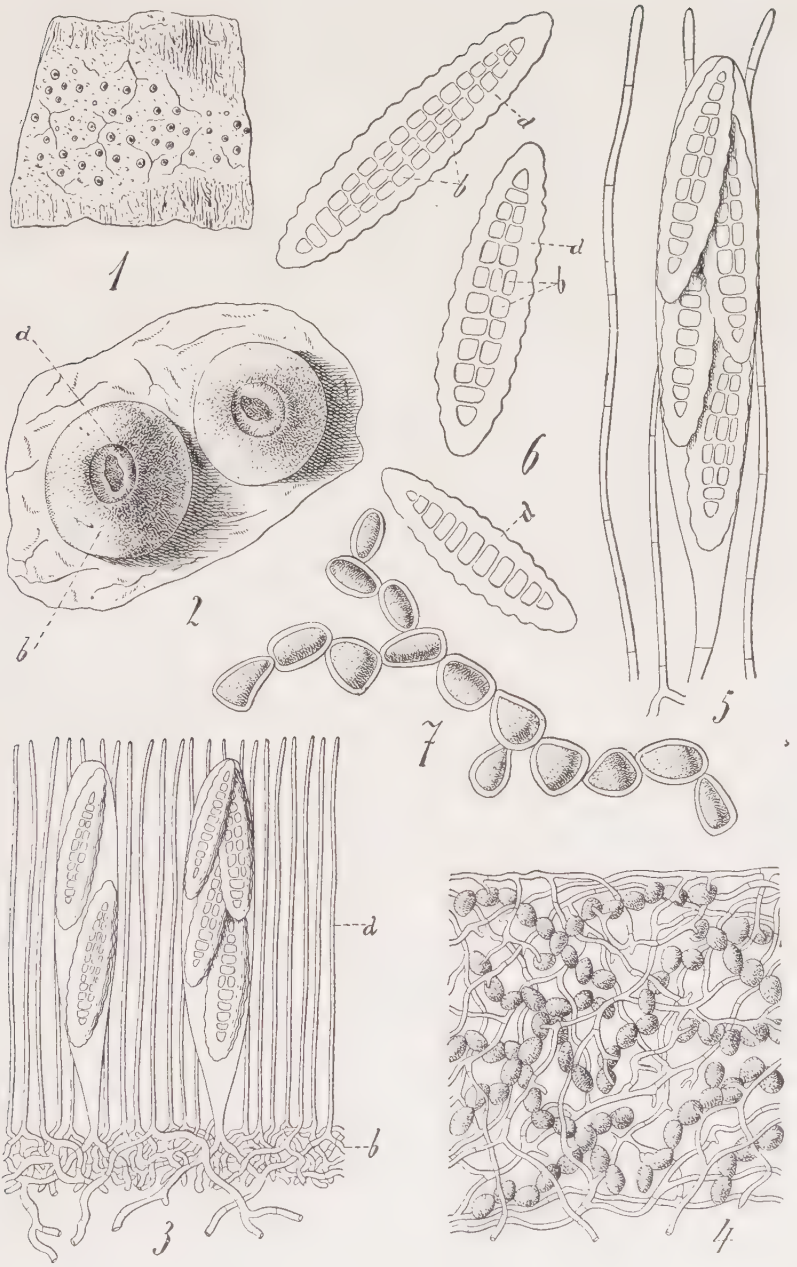

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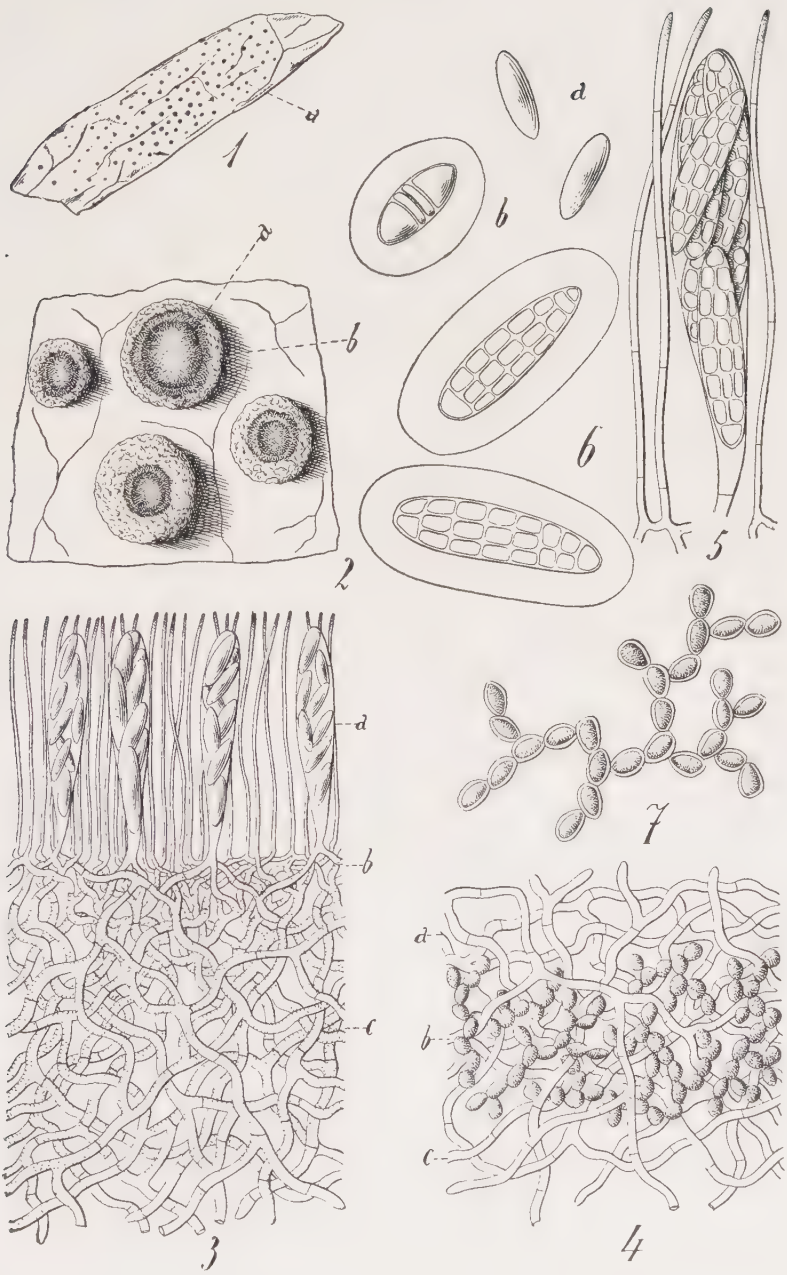

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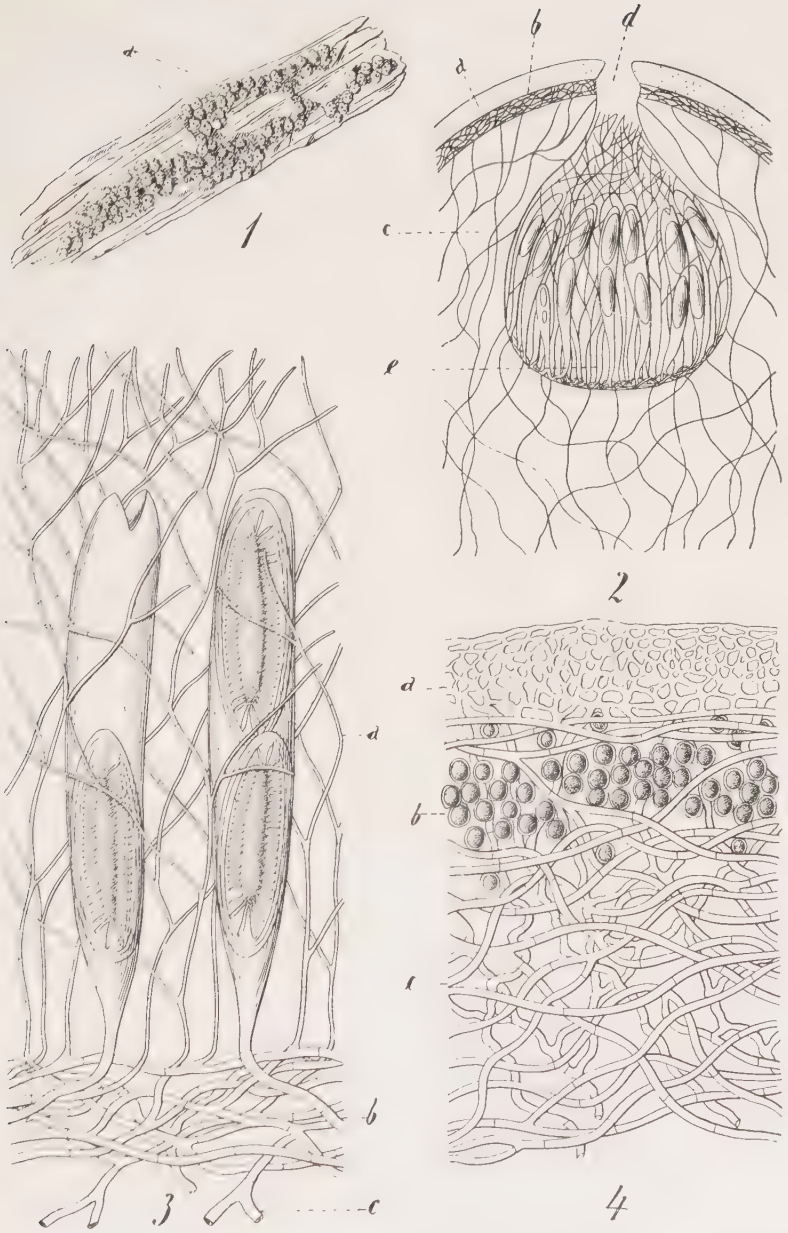

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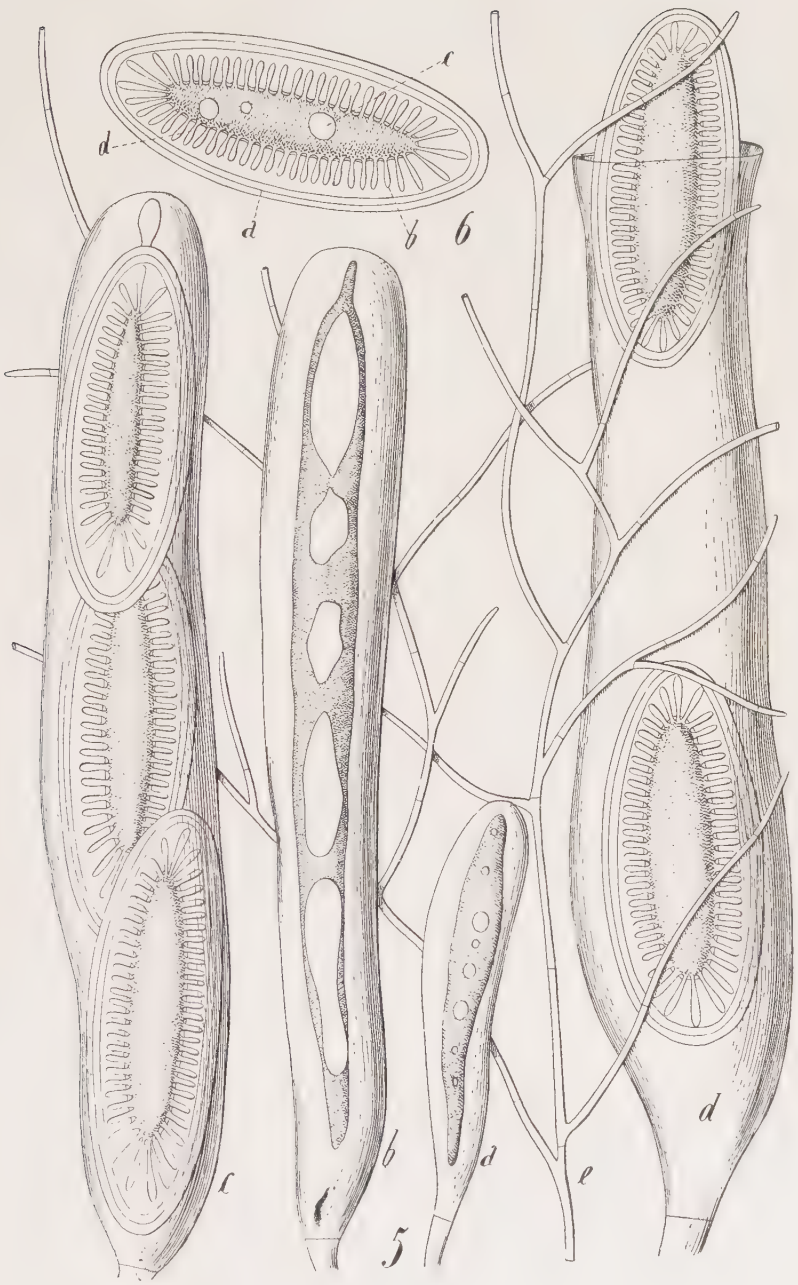

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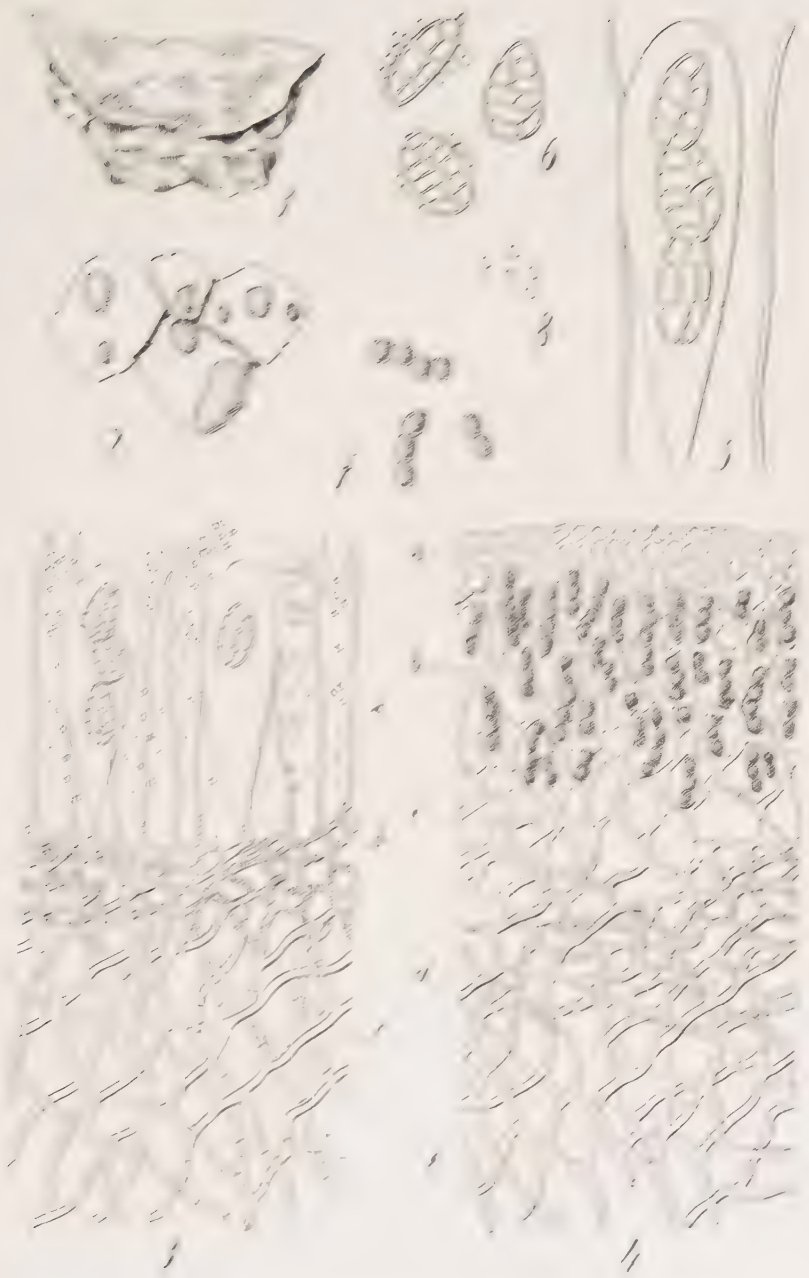

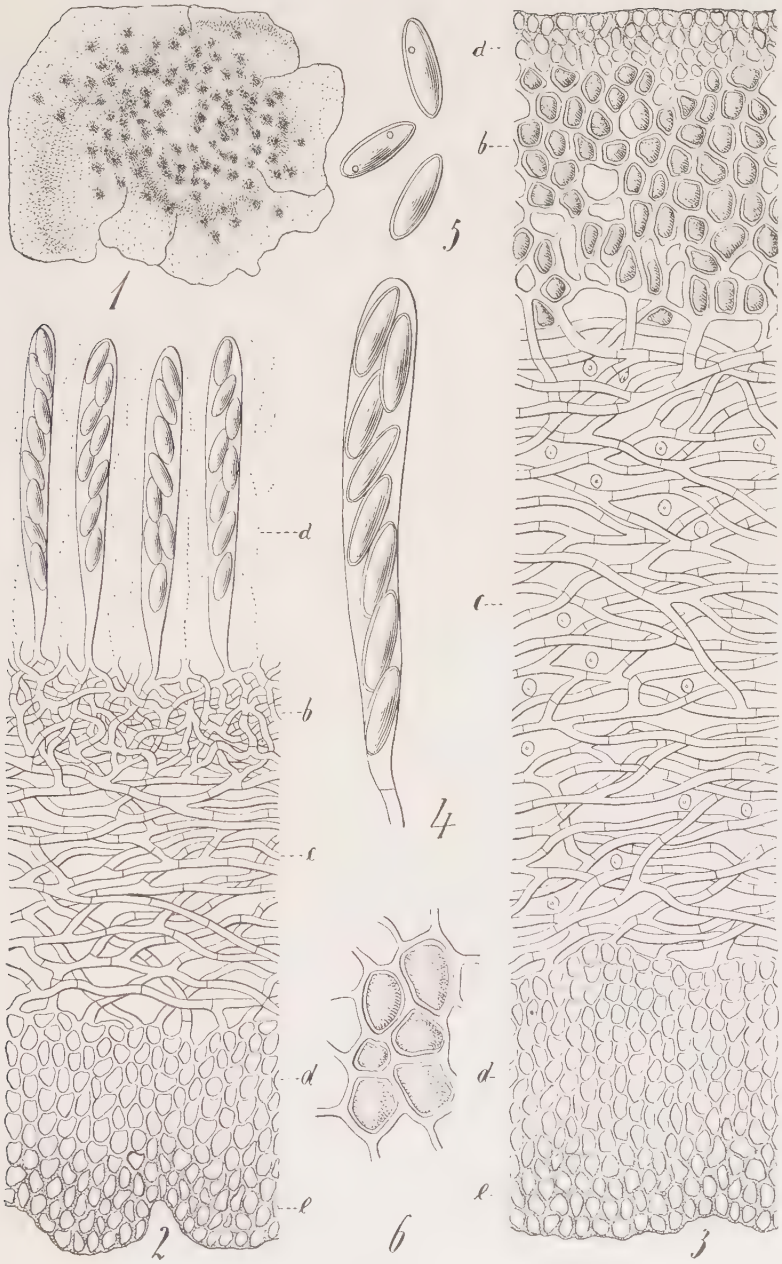

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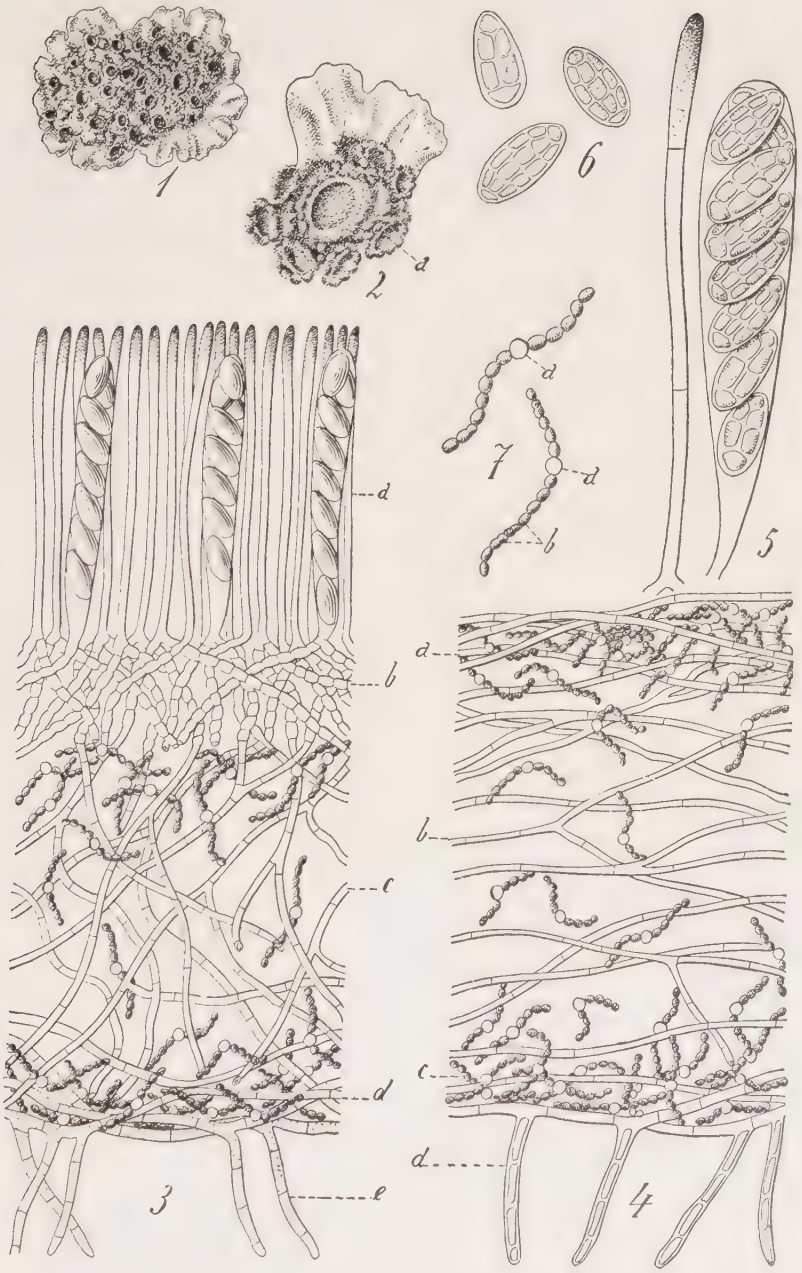

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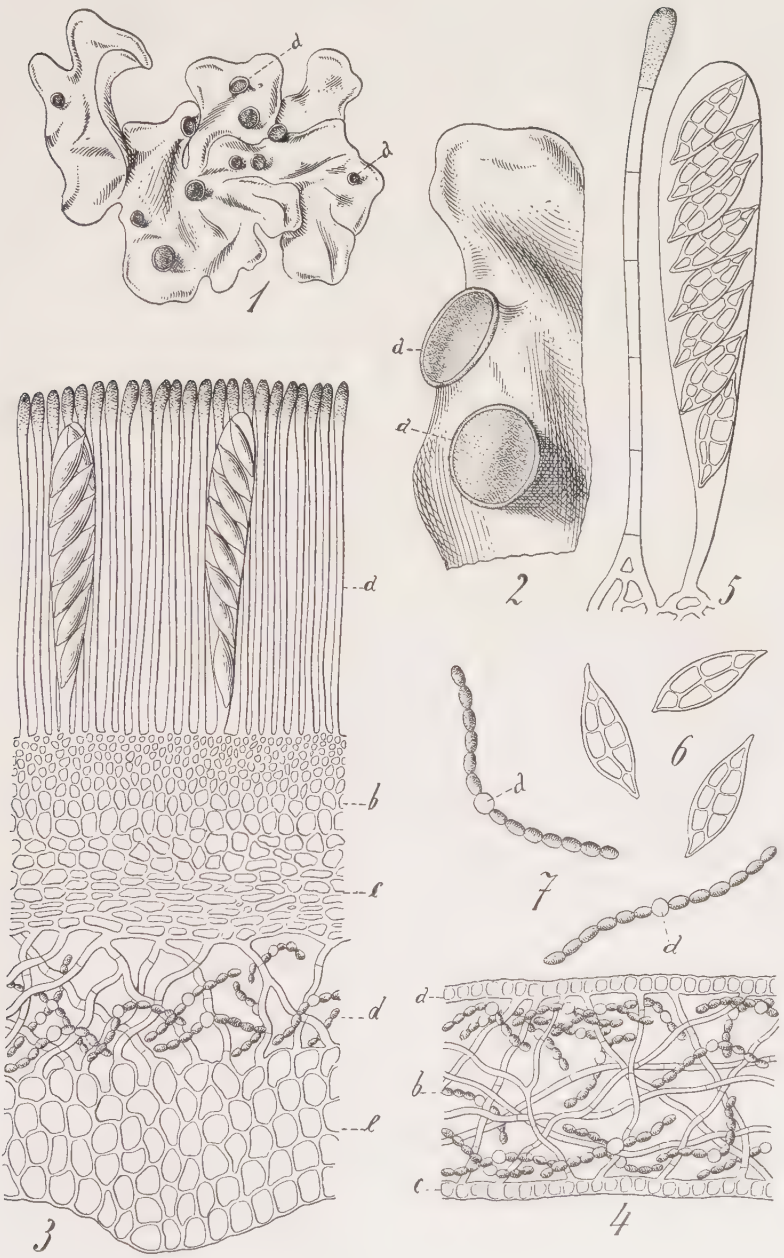

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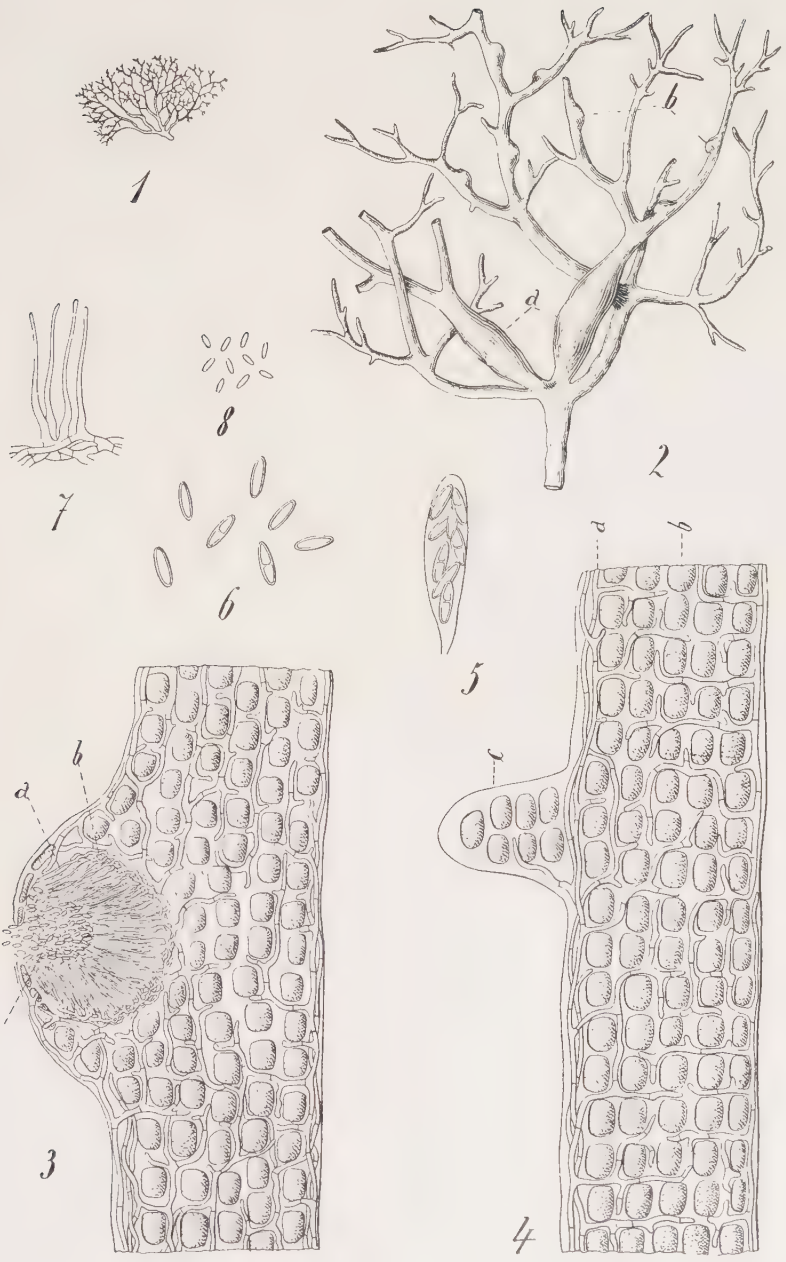

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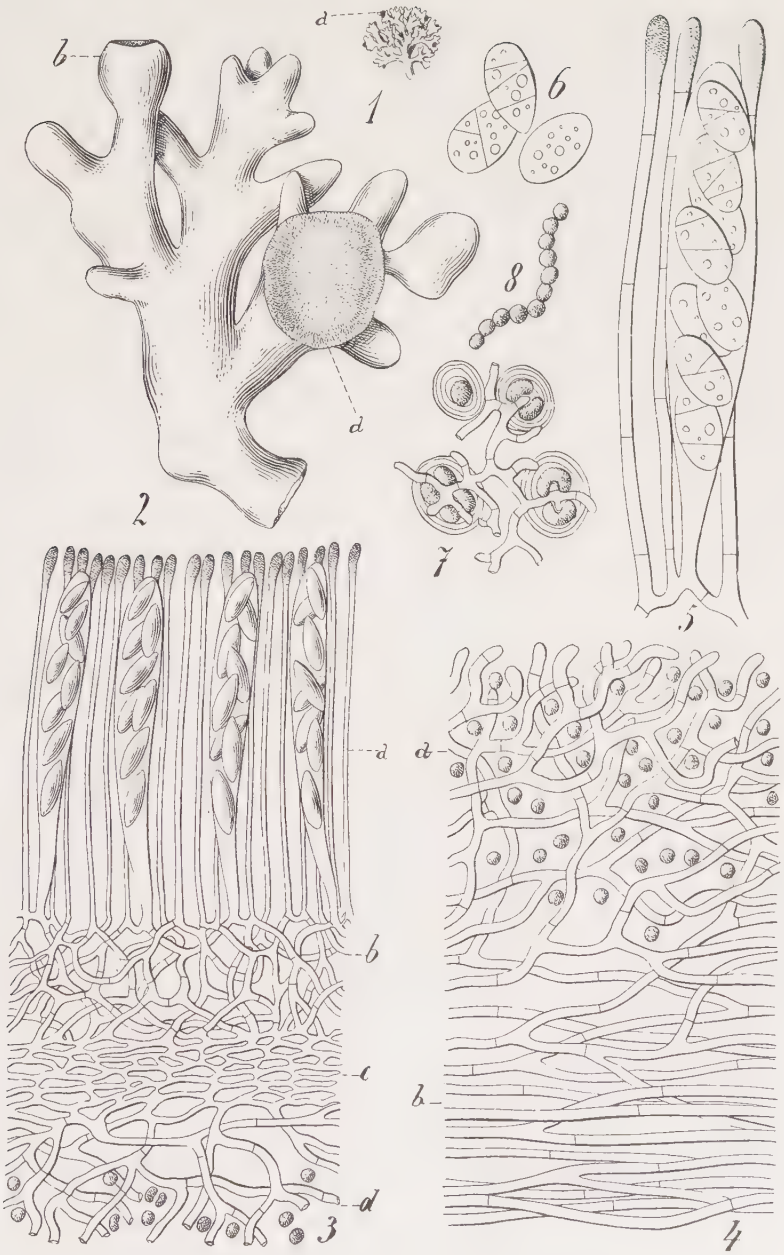

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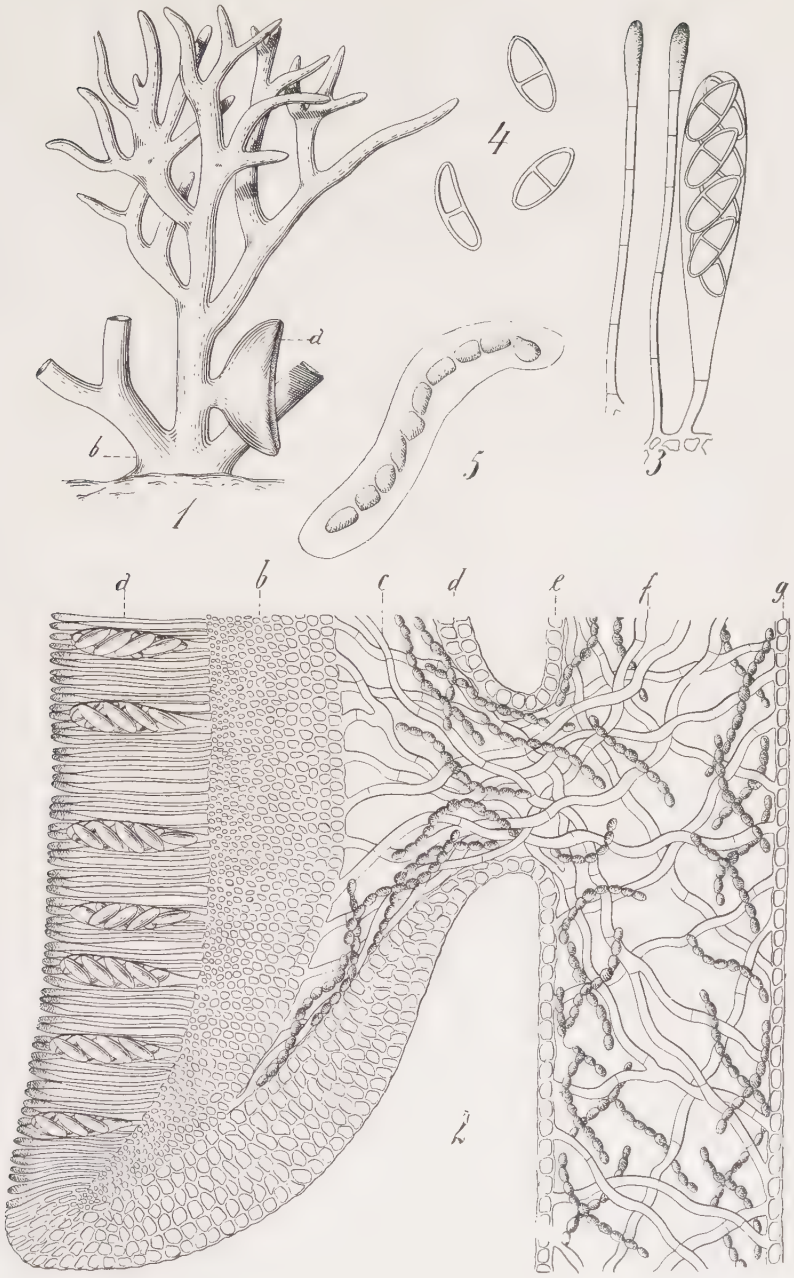

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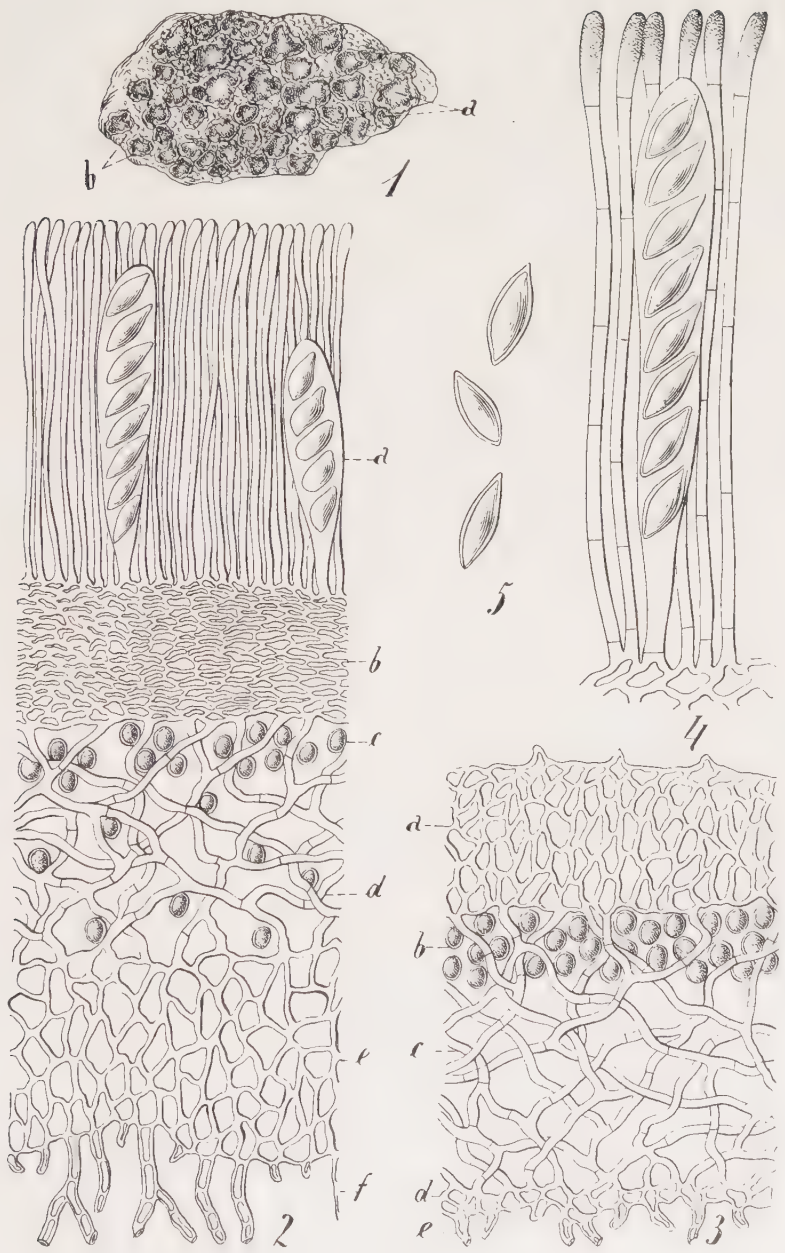

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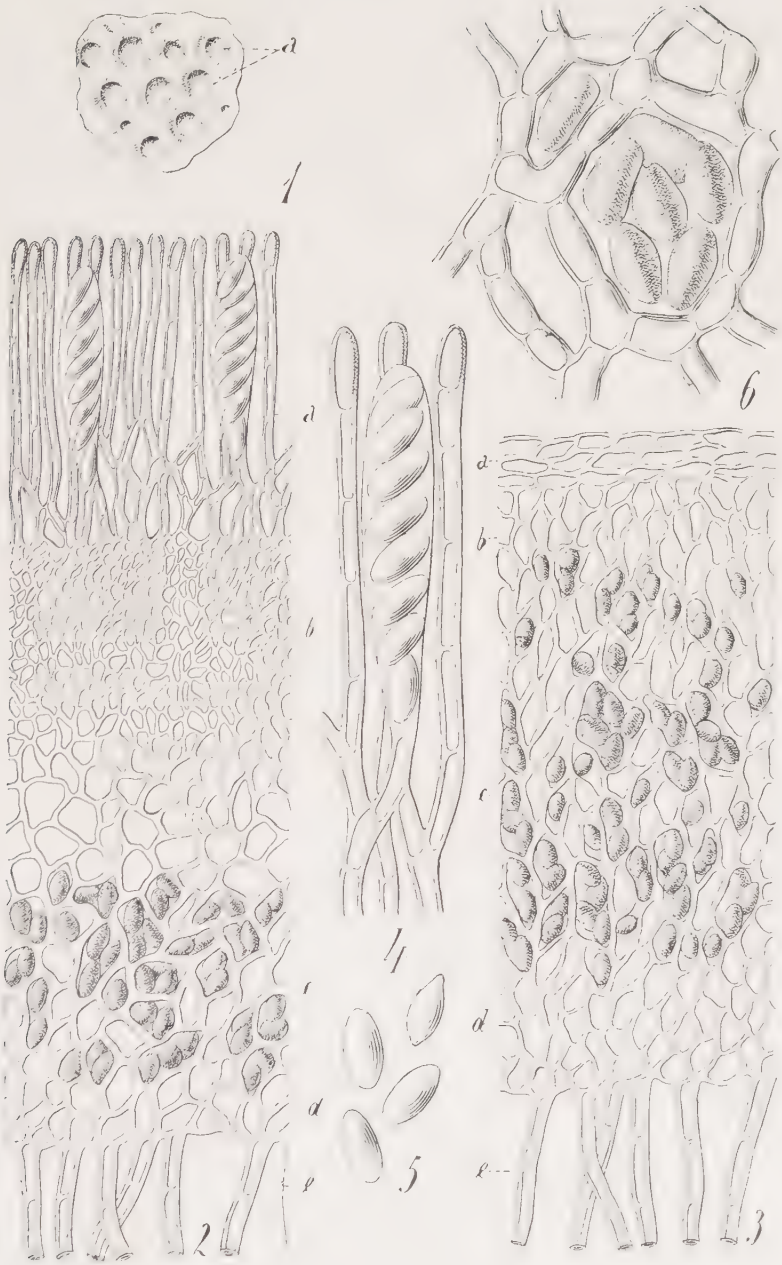

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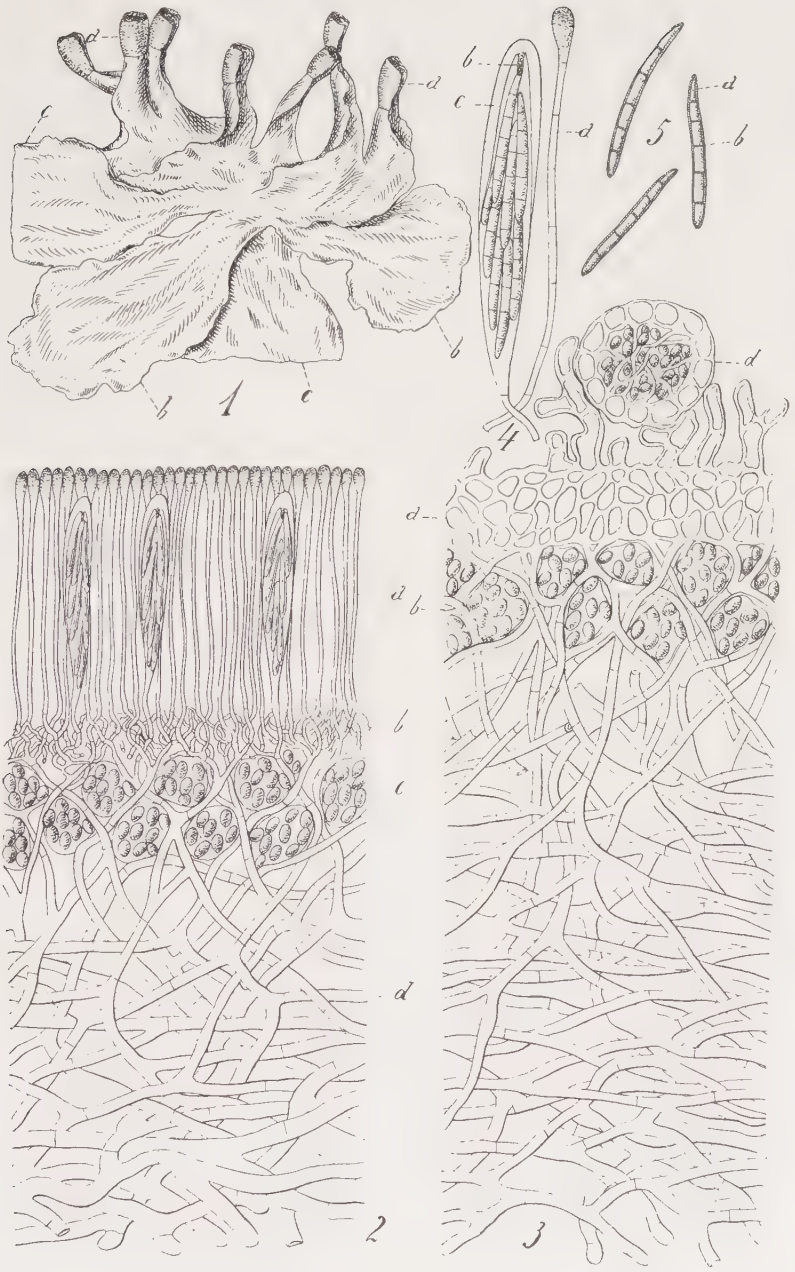

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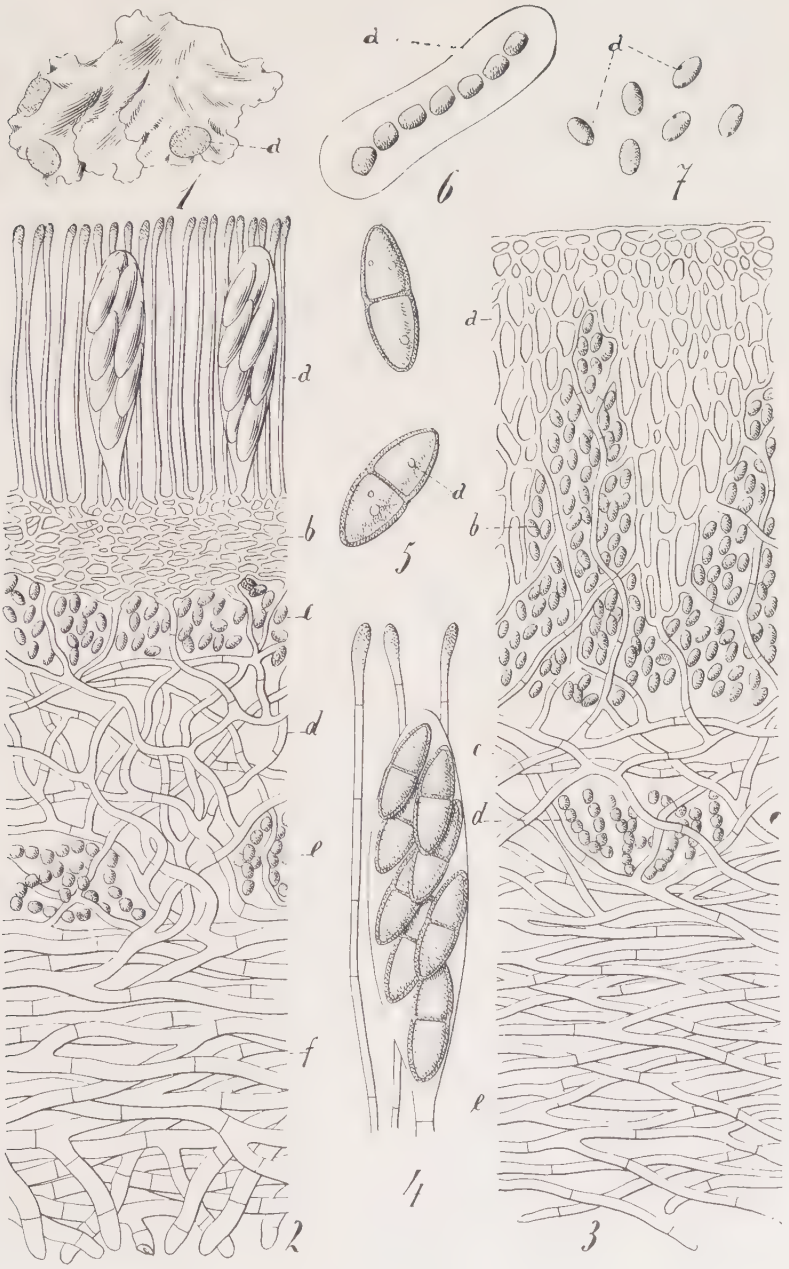

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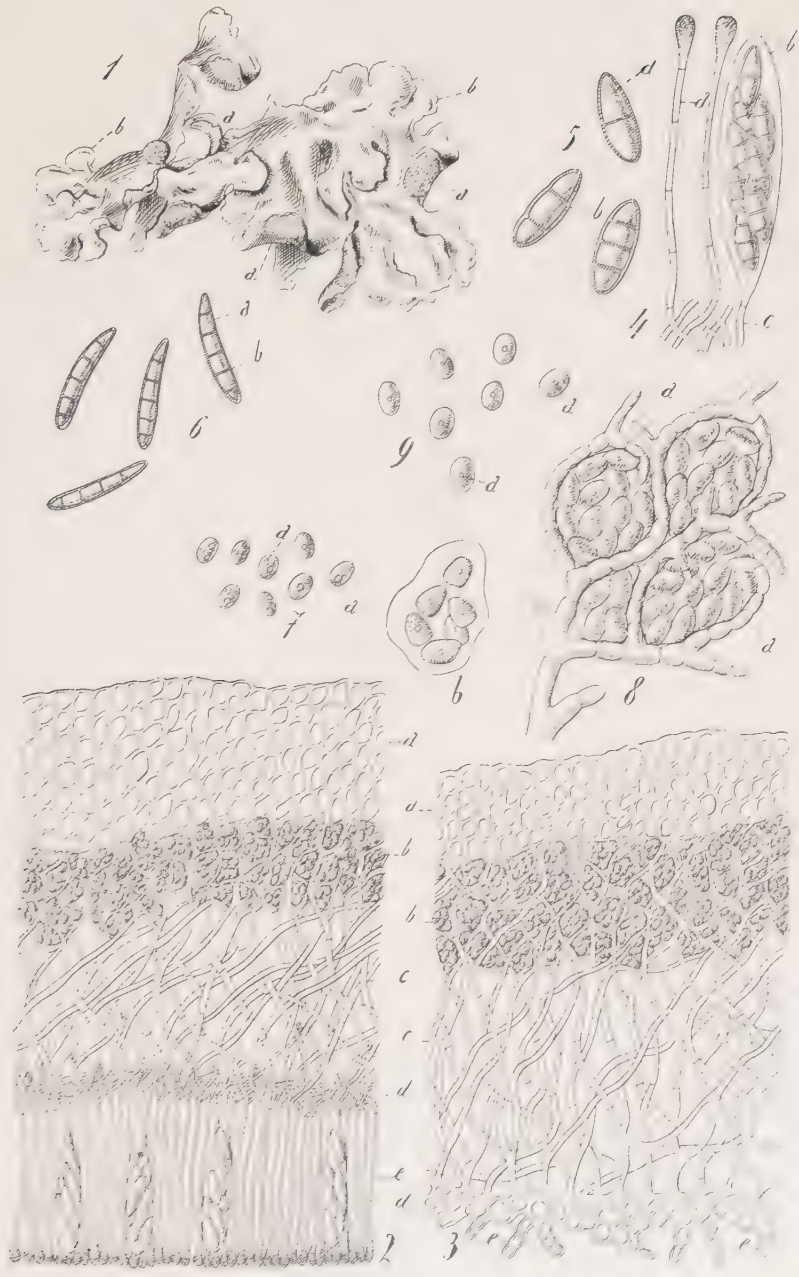

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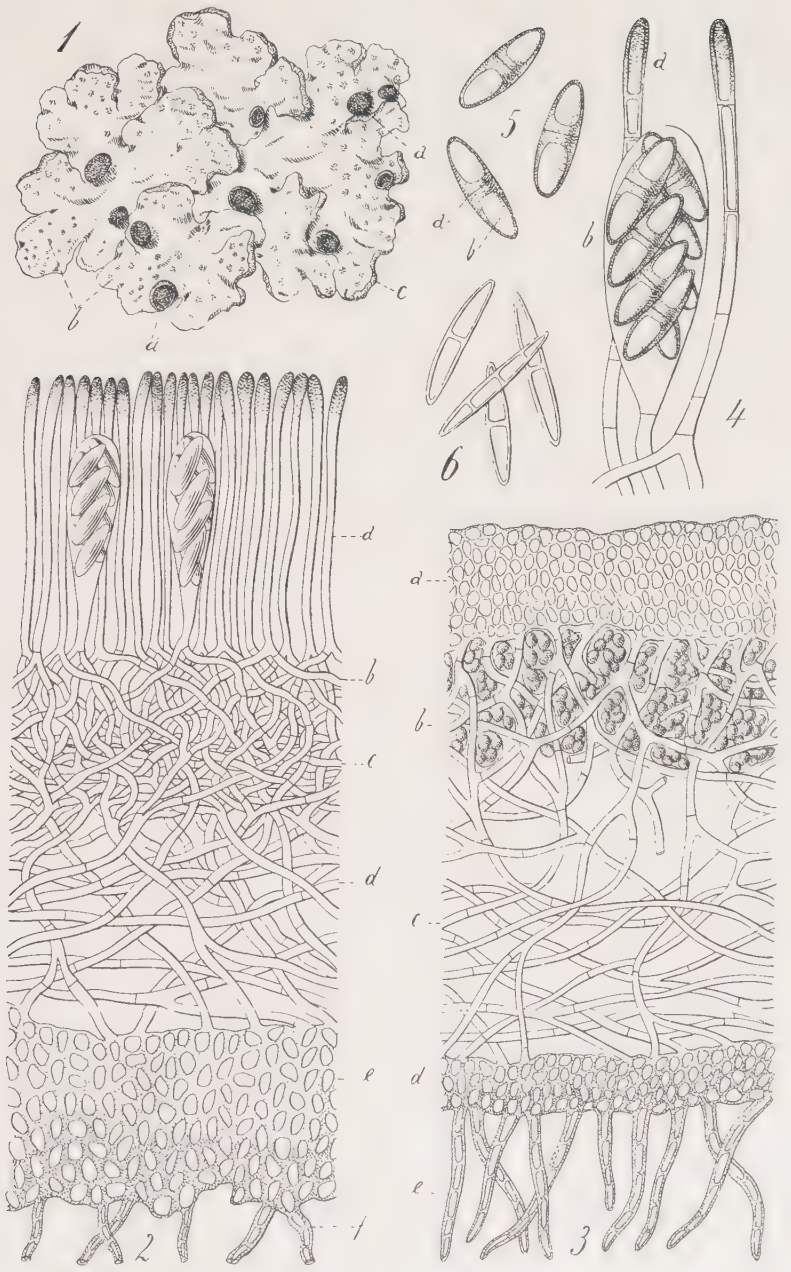

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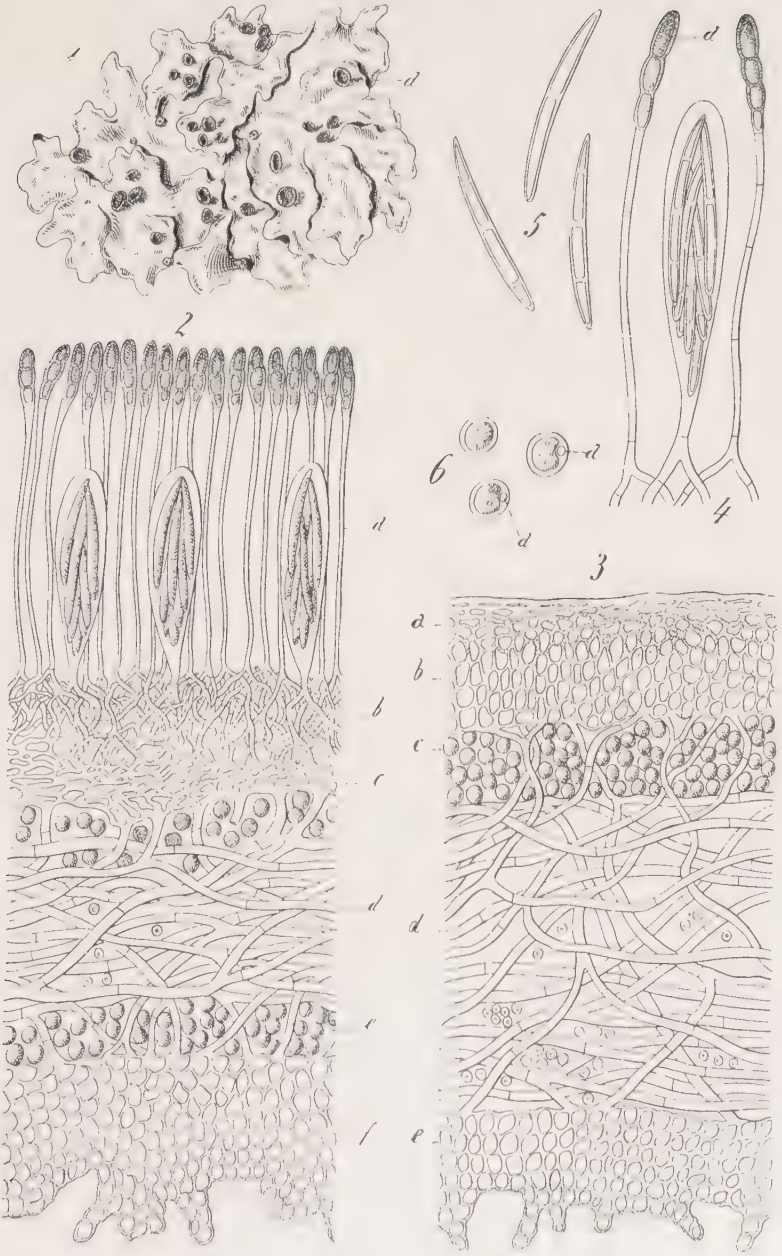

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